Diversity and Commonality in Animals

Masaharu Motokawa
Hiroshi Kajihara *Editors*

Species Diversity of Animals in Japan

Zoological Society of Japan
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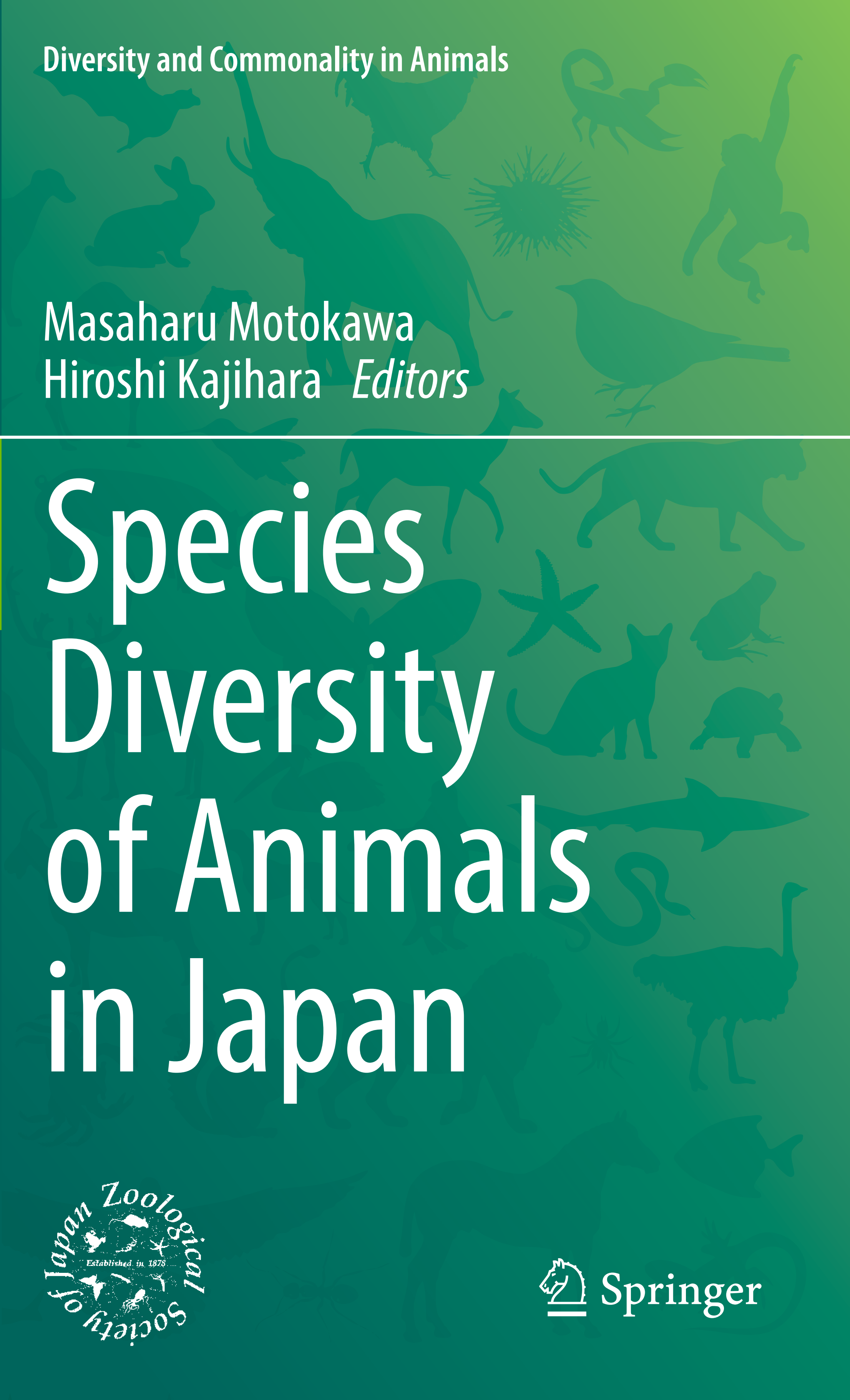

Diversity and Commonality in Animals

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Preface

Consisting of some 6800 islands and extending approximately 3500 km from north (45.6°N) to south (20.4°N), the Japanese archipelago along the eastern periphery of the Eurasian continent has had a complex geological history since the Miocene (ca. 23 million years ago), with a variety of terrestrial and marine habitats harboring a rich flora and fauna (Chap. 1). The Japanese fauna has a high proportion of endemic species, e.g., 52 % for non-flying terrestrial mammals (Chap. 3), 47 % for land birds (Chap. 4), 83 % for reptiles (Chap. 5), and 92 % for amphibians (Chap. 6). Regrettably, anthropogenically mediated habitat loss and disturbance have resulted in the extinction of a number of endemic Japanese species, subspecies, or populations, e.g., the Japanese wolf (*Canis lupus*), the Japanese sea lion (*Zalophus japonicus*), the Japanese crested ibis (*Nipponia nippon*), and the Japanese river otter (*Lutra lutra*). More than half the natural mudflats along Japanese coasts have been reclaimed, mostly for agriculture or industry, causing local extinctions—many of which have perhaps gone undetected—of small marine or estuarine organisms such as polychaetes (Chap. 19). It is important for our generation to bequeath our precious natural heritage to future generations, and therefore it is vital that scientists engaged in biodiversity research disseminate the knowledge they obtain to the general public, not only domestically but also globally. The first step toward this goal is to compile a species list through solid, steady alpha-taxonomic work in each taxon (Chaps. 6, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, and 27). Furthermore, for a deeper understanding of the Japanese fauna, it is crucial to elucidate the phylogeography and population genetic structure of each species (Chaps. 3, 5, and 6), and these results should form the basis for conservation policies and strategies (Chaps. 6, 19, and 27). Another threat to the native fauna is the problem of alien or introduced species (Chaps. 6 and 22).

In 2013, Okinawa in far-southern Japan was selected as the venue for the 22nd International Conference of Zoology (ICZ) in 2016, to be held jointly with the 87th Meeting of Zoological Society of Japan (ZSJ, founded in 1878). The Library/Publishing Committee of ZSJ, at the time under the chairmanship of Professor Kazufumi Takamune (Kumamoto University), then initiated a project aimed to facilitate the global dissemination of information on the activities of Japanese zoologists and the current status of zoology in Japan, to commemorate the occasion of the ICZ–ZSJ joint meetings. This project would entail the publication of a series of books under the title *Diversity and Commonality in Animals*, featuring research conducted by members of ZSJ in various fields of zoology, including physiology, endocrinology, neuroscience, ethology, developmental biology, evolution, reproductive biology, taxonomy, and ecology. MM (mammalian systematics) and HK (marine invertebrate systematics), representing the Kinki and Hokkaido Branches of ZSJ, respectively, were Library/Publishing Committee members in the early planning stages of the publication project and were subsequently appointed as the editors of a volume pertaining to biodiversity, which emerged as this book, *Species Diversity of Animals in Japan*.

There are 23 nationwide academic societies in Japan with members engaged in animal diversity research to various extents (approximate membership shown in parentheses): Arachnological Society of Japan (300), Carcinological Society of Japan (300), Coleopterological Society of Japan (700), Japanese Association of Benthology (400), Japan Society of Protistology (200), The Acarological Society of Japan (250), The Biogeographical Society of Japan (300), The Ecological Society of Japan (3800), The Entomological Society of Japan (1400), The Herpetological Society of Japan (400), The Ichthyological Society of Japan (1300), The Japanese Coral Reef Society (600), The Japanese Nematological Society (240), The Japanese Society of Soil Zoology (310), The Japanese Society of Systematic Zoology (400), The Lepidopterological Society of Japan (1400), The Malacological Society of Japan (800), The Mammal Society of Japan (1100), The Ornithological Society of Japan (1200), The Plankton Society of Japan (600), The Palaeontological Society of Japan (1100), The Society of Evolutionary Studies, Japan (1300), and The Zoological Society of Japan (2300).

ZSJ has fewer specialist members (i.e., acarologists, arachnologists, crustacean researchers, ecologists, entomologists, herpetologists, ichthyologists, malacologists, mammalologists, nematologists, and paleontologists) than any of the corresponding specialized societies—in other words, Japanese researchers participating in biodiversity research do not have a single platform. To help overcome this organizational deficiency, The Union of Japanese Societies for Natural History was founded in 1995, and The Union of the Japanese Societies for Systematic Biology in 2002, to coordinate the activities of those academic societies engaged in research in natural history and systematics. This coordination includes capacity-building for natural history museums and specimen storage, improvement of global species-diversity information facilities, and the enhancement of young researchers. As a consequence, networks of researchers and the knowledge of animal species diversity in Japan have been greatly enhanced in the last two decades.

The intent of this book is to summarize and provide the status quo of our knowledge of the biodiversity of the major groups of terrestrial, freshwater, and marine animals in Japan. Each chapter is written by a leading current specialist in the field. In well-studied groups such as vertebrates, the topics are treated in terms of the process of the formation of the faunas in geological time, i.e., during the Quaternary period (Chaps. 1, 3, and 5), as well as the biogeographic patterns of community composition (Chap. 4). On the other hand, a number of taxa remain poorly investigated, mostly among marine invertebrates (Chaps. 2, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, and 27) but also in terrestrial and freshwater groups (Chaps. 8, 9, 10, 11, and 12).

The authors of each chapter in this book are members of ZSJ and/or active contributors to the society's periodical journals, *Zoological Science* and *Zoological Letters*. They range in stage of career from young postdocs (Chaps. 9 and 20) to professors emeritus (Chaps. 17, 26, and 27), and were chosen as specialists in major groups of animals. The following phyla are not covered in this book: Placozoa, Ctenophora, Platyhelminthes, Orthonectida, Gnathostomulida, Gastrotricha, Rotifera, Phoronida, Brachiopoda, Chaetognatha, Cycliophora, Micrognathozoa, Mollusca, Nematomorpha, Priapulida, Loricifera, Onychophora, Xenacoelomorpha, and Hemichordata. Completeness in taxonomic coverage at the phylum level was hampered largely due to the absence or paucity of experts in ZSJ (e.g., Mollusca) or of the animals themselves in Japan (e.g., Cycliophora, Micrognathozoa, Onychophora). Future studies and collaborations are expected to fill the gap, and we hope that this book will stimulate future research.

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Part I
Introduction

Chapter 1
“Land Emergence” and “Elevation Shift” Affect Diversification: A New Perspective Toward Understanding the High Species Diversity of Terrestrial Animals in Japan

Masaharu Motokawa

Abstract Animal species in Japan are characterized by a high degree of endemism. Recent phylogeographic studies have revealed interesting and unexpected patterns of diversification in the islands adjacent to the main Japanese islands (Hokkaido, Honshu, Shikoku, and Kyushu) and the within-island diversification in the main islands. In this chapter, I propose two potential models to explain such diversification: ‘land emergence’ effects and ‘elevation shift’ effects, based on changes in animal distribution in response to climate or habitat alteration during the repeated glaciation and post-glaciation periods in the Pleistocene era. In the land emergence effect, population expansion and contraction in response to land emergence and disappearance contributed to the dynamic changes in morphological and genetic characters in the four main islands and their adjacent offshore islands. In the elevation shift effect, ‘cryptic barriers’ and ‘cryptic corridors’ were formed through elevation shifts in response to climatic changes in the past. The effect also contributed to the formation of diversification patterns among the low elevation species. For further understanding of diversification of Japanese animals, both land emergence and elevation shift effects should be evaluated for each species, with careful consideration of the ‘connectivity’ of animal dispersal.

Keywords Zoogeography • Glaciation period • Land emergence effect • Land bridge • Elevation shift effect • Cryptic barrier • Cryptic corridor • Connectivity • Island syndrome

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1.1 Introduction

Japan is a biodiversity hotspot harboring many endemic species of terrestrial animals. The landmass (378,000 km^2) of Japan consists of an island chain, including 6400 islands that lie between 122°56′–153°59′E and 20°25′–45°33′N, in subtropical and cool-temperature zones (Fig. 1.1). The high degree of endemism of Japanese terrestrial animal species is thought to have resulted from the geological formation of the Japanese Islands and the Ryukyu Islands in the Miocene period, and from many factors related to the isolation of these species, and also from the adaptation and speciation in various environments found in the Japanese Islands and the Ryukyu Islands (e.g., Dobson 1994; Dobson and Kawamura 1998; Ota 1998, 2000; Abe 1999; Millien-Parra and Jaeger 1999; Motokawa 2009, 2015).

Comparison of the land area and maximum elevation of the islands and continental areas in and around Japan in East Asia (east to 110°E) is depicted in Fig. 1.1 and Table 1.1. Honshu is the largest island in the East Asian region (seventh largest in the world), and the maximum elevation is 3776 m at Mt. Fuji in the central part. East Asia as a whole has many islands, from small to large in area, that range in elevation from low and flat to high and steep. Both the islands and the continent have very diverse geomorphological features.

With respect to animal fauna, Japan can be divided into two major biogeographic zones. The Japanese Islands, consisting of Hokkaido, Honshu, Shikoku, Kyushu, and the surrounding small islands and island groups (Sado Island, Oki Group, Tsushima Island, Izu Group, Osumi Group), are considered to represent the Palearctic element, whereas the Ryukyu Islands of the central (Amami and Okinawa Groups) and southern (Miyako, Yaeyama, and Senkaku Groups) Ryukyu Islands represent the Oriental element. The boundary between these two regions is between Akusekijima Island and Kodakarajima Island of the Tokara Group, at the deep Tokara Tectonic Straits (Tokara Gap) and where the Kuroshio Current crosses the Ryukyu Islands chain from the west to the east (Hikida et al. 1992; Hikida and Ota 1997; Ota 1998; Motokawa 2000). This major faunal division is strongly related to the geological formation and history of the Japanese Islands and the Ryukyu Islands (Kizaki and Oshiro 1977, 1980; Kimura 1996; Osozawa et al. 2012), and this significant biogeographic boundary has been called Watase's Line in recognition of Prof. Shozaburo Watase of the Imperial University of Tokyo (Kuroda 1931).

The isolation pattern of the Ryukyu Islands fauna has a strong association with the formation of each island (or island group) and the long isolation of the islands. Therefore, the animal species in the Ryukyu Islands provide good examples of vicariant speciation in islands (Ota et al. 1993; Hikida and Ota 1997; Ota 1998; Hikida and Motokawa 1999; Motokawa 2000; Osozawa et al. 2013, 2015). Recent studies on species taxonomy, distribution, and molecular phylogeny additionally elucidated the differentiation between the central and southern Ryukyus separated by the Kerama Gap (Fig. 1.1). There exists a high level of endemism in the central Ryukyus, separated by the Tokara Gap in the north and the Kerama Gap in the south (Ota 1998; Motokawa 2000; Osozawa et al. 2013).

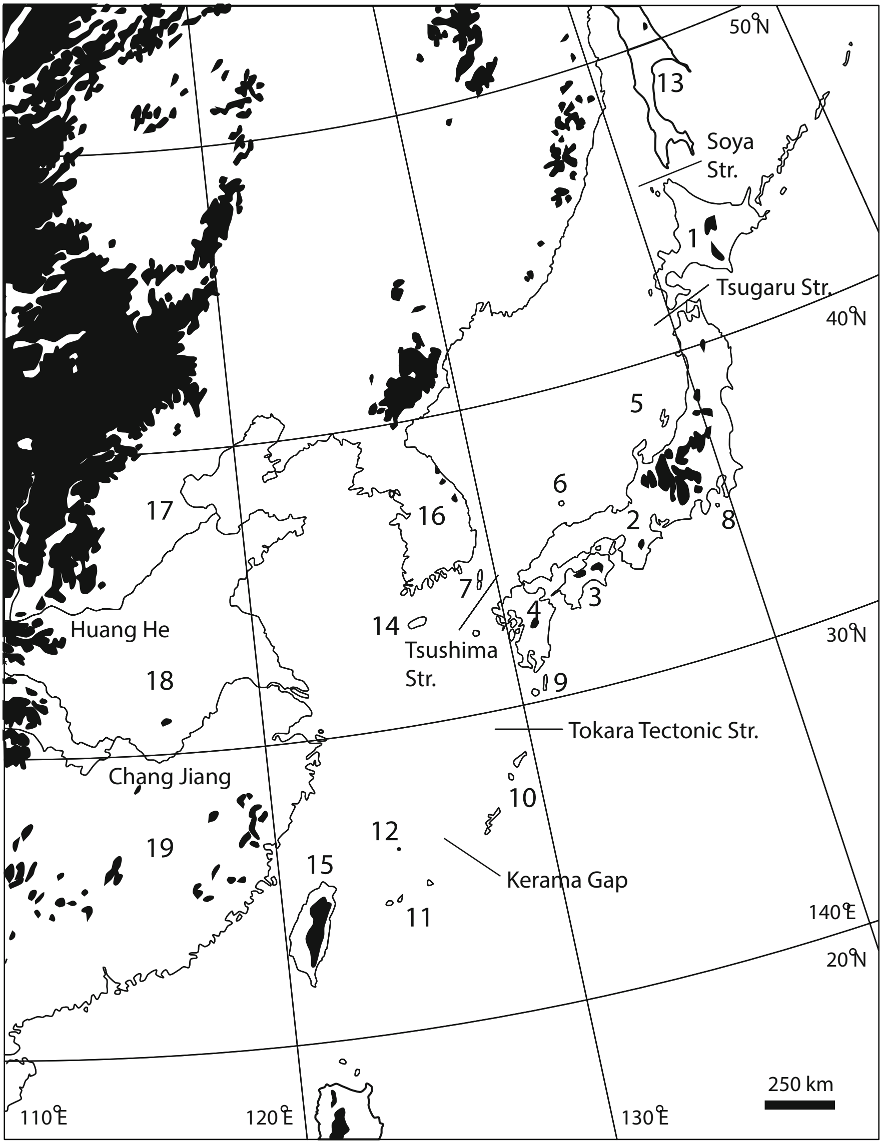

Fig. 1.1 Map of East Asia east to 110°E. *Black* area indicates mountains more than 1000 m in elevation. *Numbers* for islands, island groups, and regions correspond to those in Table 1.1

In contrast, the patterns of the fauna of the Japanese Islands, including the four main islands of Hokkaido, Honshu, Shikoku, and Kyushu, appear much more diverse among species. Several animal species, including mammals and insects (Sato 2016 Chap. 3; Tojo et al. 2016 Chap. 8), have been isolated since the Miocene when the Japanese islands split from the eastern part of the continent

Table 1.1 Geographic regions, areas, and maximum elevations of the East Asian islands and the continent east of 110°E

	Region	Area (km^2)	Elevation (m)
1	Hokkaido	77,978	2290
2	Honshu	227,895	3776
3	Shikoku	18,292	1982
4	Kyushu	36,716	1791
5	Sado Island	854	1172
6	Oki Group	242	608
7	Tsushima Island	696	649
8	Izu Group	24	432
9	Osumi Group–Tokara Group	505	1936
10	Amami Group–Okinawa Group	712	694
11	Miyako Group–Yaeyama Group	222	526
12	Senkaku Group	4	362
13	Sakhalin	76,400	1609
14	Jeju Island	1,840	1950
15	Taiwan	35,873	3997
16	Korean Peninsula	–	2750
17	Northern continent	–	3058
18	Mid-latitude continent	–	3105
19	Southern continent	–	2158

The area and elevation data are for the highest island in each island group, indicated as follows: 6, Dogo Island; 8, Niijima Island; 9, Yakushima Island; 10, Amamiohshima Island; 11, Ishigakijima Island; 12, Uotsurijima Island

and thus exhibit high levels of endemism. However, many other species are thought to have migrated from the continent to the Japanese Islands, or from the main islands to the adjacent islands, via the Pleistocene land bridge (Kawamura 2007; Kawamura and Nakagawa 2012; Sato 2016 Chap. 3).

Tokuda (1941a), of Kyoto Imperial University, wrote a pioneering book on the origin of Japanese terrestrial animals entitled *Nihon Seibutsu Chiri* ("Biogeography of Japan"), based on his thesis research on the taxonomy of murid rodents in East Asia (Tokuda 1941b). Tokuda (1941a) stressed the importance of isolation and land bridge formation in producing new species or subspecies. His views (Tokuda 1941a) greatly impacted the study of the biogeography of Japanese animals. He established the sequence and time of formation of each strait, such as Soya Strait between Hokkaido and Sakhalin (as a northern migration route from the continent), Tsugaru Strait (as a faunal boundary between Honshu and Hokkaido, often called Blakiston's Line), and Tsushima and Korean Straits (as western migration routes from the continent), and each was discussed to reveal and explain the patterns of fauna in the main Japanese islands. The current perspective on the last glaciation period is that the Honshu–Shikoku–Kyushu landmass did not connect with the Korean Peninsula and Hokkaido, although Hokkaido had a land bridge with the northeastern continent. In addition to the main islands connecting with the continent, the isolation of small islands adjacent to the main Japanese islands, and the time and sequence of the formation of the relevant straits, are also important. Geological changes and sea level changes were used to estimate the formation of straits (or isolation of islands) and land connections (Ohshima 1990, 1991). Since Tokuda (1941a), most researchers have tried to explain the formation of island fauna in line with the last formation of the strait (vicariant events) that provided the routes for migration to the main Japanese islands from the continent, as well as to the adjacent small islands from the main Japanese islands.

Recent molecular phylogeographic studies, however, have revealed more complicated features for the geographic divergence in Japanese animals, with two particular issues: (1) in small islands adjacent to the main Japanese islands, genetic divergence and phylogeographic patterns were not concordant with the prevailing hypothesis for the formation of the strait and the land bridge; and (2) several species showed unexpected divergence within the main Japanese islands.

In work that elucidated the vicariance patterns of amphibians and reptiles in the Ryukyu Islands, Ota (1998) made four a priori assumptions: (1) currently recognized genera, species, and subspecies are monophyletic unless otherwise claimed; (2) in fairly small islands, such as those of the Ryukyus, the within-island diversification of a given species or subspecies is negligibly small compared to its between-island diversification; (3) recognizable phylogenies initiate only through between-island vicariance; (4) and lineages showing apparent disjunct distributions with their sister lineages are relict at their taxonomic levels sensu Darlington (1957). Of these four assumptions, points (2) and (3) are unlikely to hold in the main Japanese islands in light of the two issues raised here.

In addition to the formation of island populations of terrestrial animals, overall changes in population size as well as morphological and genetic diversification in island populations have been studied worldwide, often termed the island rule or island syndrome (Adler and Levins 1994; Lomolino 2005; Meiri et al. 2008; Lomolino et al. 2012, 2013), as being caused by the short-term or long-term effects of isolation (Whittaker 1998). However, the two issues observed in the Japanese Islands might not be explained by only the effects occurring after the isolation of the island, and new explanations should be developed.

Motokawa (2014) pointed out the necessity to reevaluate the so-called land bridge as a new concept, considering that it formed in the glaciation period as a consequence of the sea level change in the Japanese islands where a huge landmass might have emerged in the glaciation period, which must have provided not only a simple passageway (land bridge) for animals (Fig. 1.2a) but also a place for temporal distribution ranges following population size expansion. Changes in distribution are expected to have resulted in morphological and genetic changes in the area that expanded from the coasts of the main islands to the adjacent islands.

In contrast, Motokawa (2008) and Shintaku and Motokawa (2016) proposed the importance of studies to elucidate the real distribution range and its changes during the Quaternary period with an example of a geographic variation study of a very common lowland murid species, the Japanese large field mouse *Apodemus speciosus*. Potential distribution ranges in the present and in the past that were

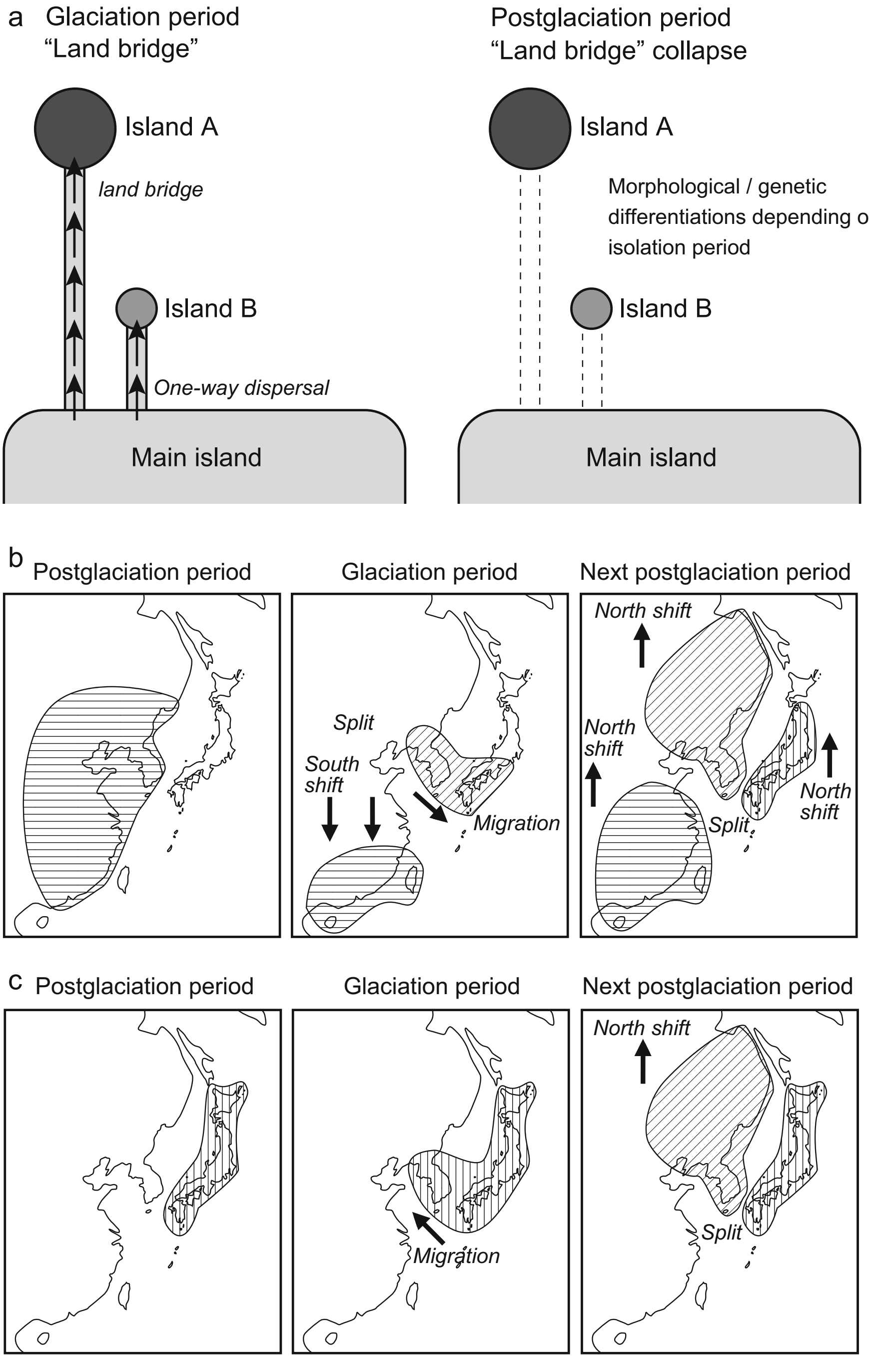

Fig. 1.2 Previous model for land bridge (modified from Hikida 2003). (**a**) Land bridge as one-way dispersal corridor. (**b**) Land bridge formation and north–south movements proposed by Hikida (2002, 2003). (**c**) Land bridge for dispersal from the main Japanese islands to the Korean Peninsula proposed by Hikida (2002, 2003)

estimated based on elevation in topographical features could recognize the existence of cryptic barriers or cryptic corridors according to the elevation distribution change under the complicated geomorphology of the main Japanese islands.

In this chapter, on the basis of these two aforementioned ideas, I propose more integrated schemes for animal divergence in the Japanese Islands, especially focused on divergence 'within' the main Japanese islands, in light of the response to 'land emergence' and 'elevation shift' during the glaciation and post-glaciation periods.

1.2 Land Bridge

Populations of terrestrial animals in islands are widely accepted to have originated and dispersed from the continent or main islands through a so-called land bridge formed in the glaciation period, especially during the Pleistocene, except for populations that are likely to have come from long-distance dispersal routes or overseas dispersal.

Speciation or differentiation in each island population, as revealed in genetic, morphological, and ecological characteristics, has been explained by vicariance and the isolation of the island.

Land bridge formation is of course a necessary basis for initially establishing the island population, although the existence of a land bridge does not directly imply migration of all animal species concerned, because some animals may not have migrated even though the land bridge had formed. Therefore, the time of the migration or last exchange of the island population can be considered to correspond with, or be earlier than, the last formation of the land bridge just before the final formation of the strait.

Hikida (2002, 2003) (Fig. 1.2b) discussed the hypothesized dispersal process through the post-glaciation and glaciation periods. Figure 1.2b shows that the population in the continent in the post-glaciation period (left) had moved to the south in the glaciation period and split into two populations (center) in (1) southern China and Taiwan, and (2) the Korean Peninsula–land bridge-formed area–western part of Japan. In the next post-glaciation period (right), populations in Korea and western Japan had split because of the collapse of the land bridge, and each of the three populations moved northward. This hypothesis is regarded as the first explanation as to how land bridge formation initiated and could be responsible for the north–south shift of animals as the result of temperature changes. Hikida (2002, 2003) also argued that the distribution changed in response to land bridge formation in the glaciation period and the reverse migration from western Japan to the Korean Peninsula (Fig. 1.2c). The movement from western Japan to the Korean Peninsula might have been initiated by the movement from the northeast to the southwest in the main Japanese islands. This model (Fig. 1.2b, c) may suggest the dynamic distribution change of terrestrial animals in the Japanese islands during the glaciation and post-glaciation periods, and it is the first hypothesis that the land bridge functioned substantially in connection with the north–south direction distribution shift rather than the predominant view that the land bridge is simply the passageway or corridor of one-way animal dispersal (Fig. 1.2a).

Modeling the land areas and potential animal distributions during repeated glaciation and post-glaciation periods during the Pleistocene for each species is important for precise understanding of the land formation effect. As the first step, I reconstructed features of animal distribution in the Japanese islands in the last glaciation maximum (LGM). This step is needed because the geomorphological changes since the LGM, such as uplift and subsidence, are thought to be small and negligible (Ota et al. 1993), and many paleo-environmental studies document the process of environmental changes. In addition, the most important point is that LGM is the last glaciation period, and traces of effects from LGM must remain in the current animal distribution and phylogeographic patterns and potentially in their genetic signature.

1.3 'Land Emergence' Effect

Shintaku and Motokawa (2016) reconstructed the current and LGM potential distribution of the Japanese field mouse *Apodemus speciosus*, considering only the factor of elevation shift. This mouse, a good model animal, is widely distributed in the Japanese Islands including the main islands (Hokkaido, Honshu, Shikoku, and Kyushu) and most adjacent islands larger than about 10 km^2 including Rishiri Island, Sado Island, the Izu Group, Oki Group, Tsushima Island, Iki Island, Osumi Group, and Tokara Group. It is commonly found in various habitats such as forests, plantations, riverside fields, paddy fields, and cultivated fields at lower and middle elevations (Shintaku and Motokawa 2016). Different patterns of divergence (Fig. 1.3) have been reported for karyotypes (Tsuchiya et al. 1973; Tsuchiya 1974), morphology (Kobayashi 1981), and the cytochrome *b* gene (Suzuki et al. 2004), and *A. speciosus* has been regarded as an example for the evolutionary study of Japanese animals (Shintaku et al. 2012; Shintaku and Motokawa 2016). Additionally, its widespread populations in various habitats offer opportunities for easy sampling to test the hypothesis.

Apodemus speciosus has rarely been recorded at high elevations with subalpine coniferous forest, and its potential distribution is thought to be lower than 1600 m (Shintaku and Motokawa 2016). In Fig. 1.4a, the white portion is the potential distribution at the present time, which is between 0 and 1600 m in elevation, whereas the black part (especially in central Honshu) is an unavailable area above 1600 m in elevation. The potential distribution of this species in the LGM is reconstructed in Fig. 1.4b, with a postulation that the altitudinal distribution may have shifted 1000 m lower than the present distribution in response to a temperature decrease of approximately 6 °C (Ota et al. 2010). The contour line for 130 m below sea level was considered the extension of the coastal line and was used to estimate the emergence of land areas in the LGM (as shown by Shintaku and Motokawa

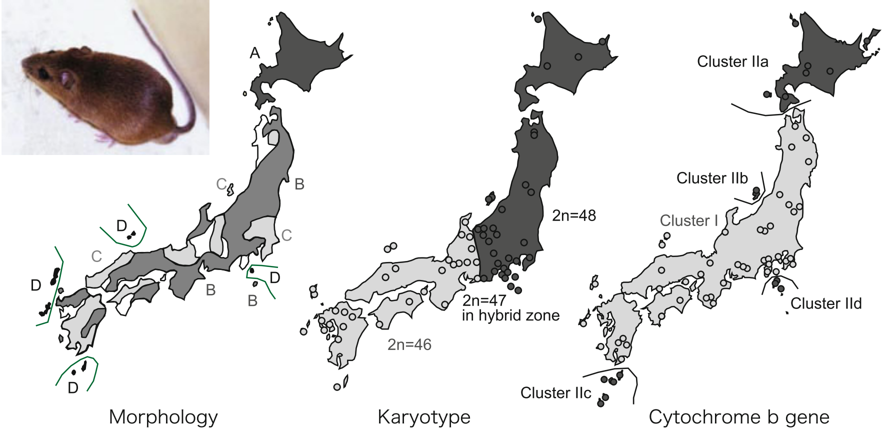

Fig. 1.3 Different patterns of divergence reported for karyotypes (Tsuchiya et al. 1973; Tsuchiya 1974), morphology (Kobayashi 1981), and cytochrome *b* gene (Suzuki et al. 2004)

2016) because the sea depth around Japan was estimated to have dropped by 120–135 m in the LGM (Ota et al. 2010). Therefore, the estimated distribution in LGM of this species (shown in white), is the estimated altitudinal range from −130 to 600 m; and the black portion is an unavailable area at more than 600 m.

In the LGM as shown in Fig. 1.4b, no land connection of the main Japanese islands with the continent was formed. Tsushima Strait and Tsugaru Strait were thought to have existed and would have separated Honshu–Shikoku–Kyushu from the Korean Peninsula and Hokkaido, respectively. However, several adjacent islands were connected with the main islands by a ‘land bridge.’

The configuration of the land connection between the main Japanese islands and the adjacent islands was variable among islands and island groups. For example, Tanegashima Island and Yakushima Island are thought to have been connected to southern Kyushu with a limited land connection, likely a narrow corridor, in the form of a so-called land bridge (Fig. 1.4b), whereas the islands located in the north of Kyushu, including Tsushima Island and Iki Island, had connected with the northern coast of Kyushu as well as the coast of the Sea of Japan in western Honshu, forming huge land areas (Fig. 1.4b). I propose that such a land connection involving many islands connecting together should be considered a land emergence rather than a land bridge. Areas of land emergence resulting from the sea level lowering are much larger than the small adjacent island(s) itself and even potentially larger than actual effective habitat/distribution range of the main island. Changes in animal distribution in the coastal region of the main islands, the adjacent islands, and the land emergence area during the glaciation and post-glaciation periods are considered in this chapter, derived from the preliminary idea provided by Motokawa (2014).

In the previous model (Fig. 1.2a), the land bridge was formed in the glaciation period and provided the narrow corridor whereby the animals could migrate from

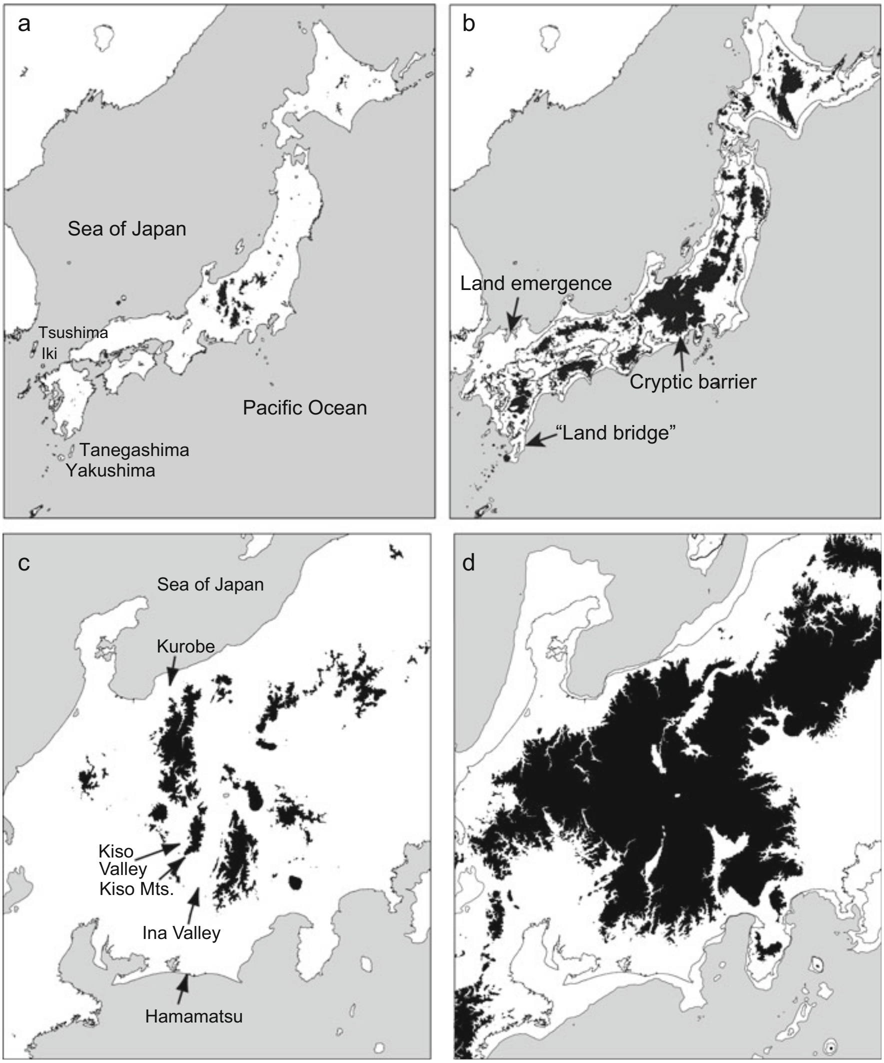

Fig. 1.4 Distribution of lowland species in the Japanese islands with *Apodemus speciosus* as a model (modified from Shintaku and Motokawa 2016). (**a**) Potential distribution (*white*) in areas less than 1600 m in elevation. (**b**) Estimated potential distribution in the last glaciation maximum (LGM) between −130 and 600 m, and ‘elevation shift’ in the central part (modified from Shintaku and Motokawa 2016). (**c**) Potential distribution in the present (*white*) in areas less than 1600 m in elevation in central Honshu. (**d**) Estimated potential distribution in LGM (*white*) between −130 and 600 m elevation in central Honshu

the main islands to the adjacent islands, mostly in a one-way direction, resulting in the formation of the adjacent island population. After the collapse of the land bridge in the post-glaciation period, the island population became isolated, resulting in morphological and genetic differentiation, depending on isolation time and island area (Fig. 1.2b). In this previous model, the land bridge functioned to provide the source of the founder population on the adjacent island as the result of migration from the main island.

My new idea, the ‘land emergence’ effect, is illustrated in Figs. 1.5 and 1.6 for repeated glaciation and post-glaciation periods. In the glaciation period when each of the islands (A and B) did not have a population of the species, animal dispersal from the main island toward the islands A and B had occurred in response to the formation of a huge land emergence (Fig. 1.5a). Dispersal from the main island coast toward the area of land emergence and corresponding areas of adjacent islands could be simple dispersal into the ‘empty’ area where the conspecific population did not exist. The elevation shift from the mountains down to the lowland had also occurred on the main island, and this shift would accelerate or drive range expansion from the mountain and low elevations into the areas of emerging land.

After the area of “land emergence” and the corresponding adjacent islands had been occupied by the animals (Fig. 1.5b), the area of land emergence declined because of sea level uplift in the post-glaciation period (Fig. 1.5c). Even though the time and rate of island shrinkage must have been variable in response to the pattern of climate change from the glaciation to the post-glaciation period, the one huge distribution area (Fig. 1.5b) finally must have split into separate populations of the main islands and the small islands (A, B) (Fig. 1.5c). During the shrinking process of the huge ‘occupied’ land area, animal populations responded to the change, and a contraction event must have occurred. The selection pressures were expected to be severe during the contraction event that led toward the split of populations into the main islands and adjacent islands. Depending on the characteristics of dispersal, sociality, habitat, life history, and locomotive ability of the concerned species, the selection pressures and associated morphological and genetic changes, as well as drift or bottleneck events, must have become variable among the species. Differentiation among the areas (for each population in the main island and adjacent islands) is expected also to reflect differential responses to the different shrinking processes experienced at each location. Additionally, in the main island, distribution of each population had expanded into the higher mountains with an up-shift in elevation in addition to the shrinkage and population contraction on the coastal side. The events just discussed occurred in the post-glaciation period. Newly formed adjacent island populations could have diverged from the main island population in morphological and genetic characters in response to the range shrinkage and population contraction, rather than the isolation-based ‘island effect’ after the isolation and formation of the island population, as discussed previously. Such events might have also caused the morphological and genetic changes in the main island populations by contraction and restructuring of the population in response to the shrinking and elevation up-shift expansion. Therefore, dynamic animal movements and population restructuring should be considered to understand the patterns of morphological and genetic variation in both main island and adjacent island populations.

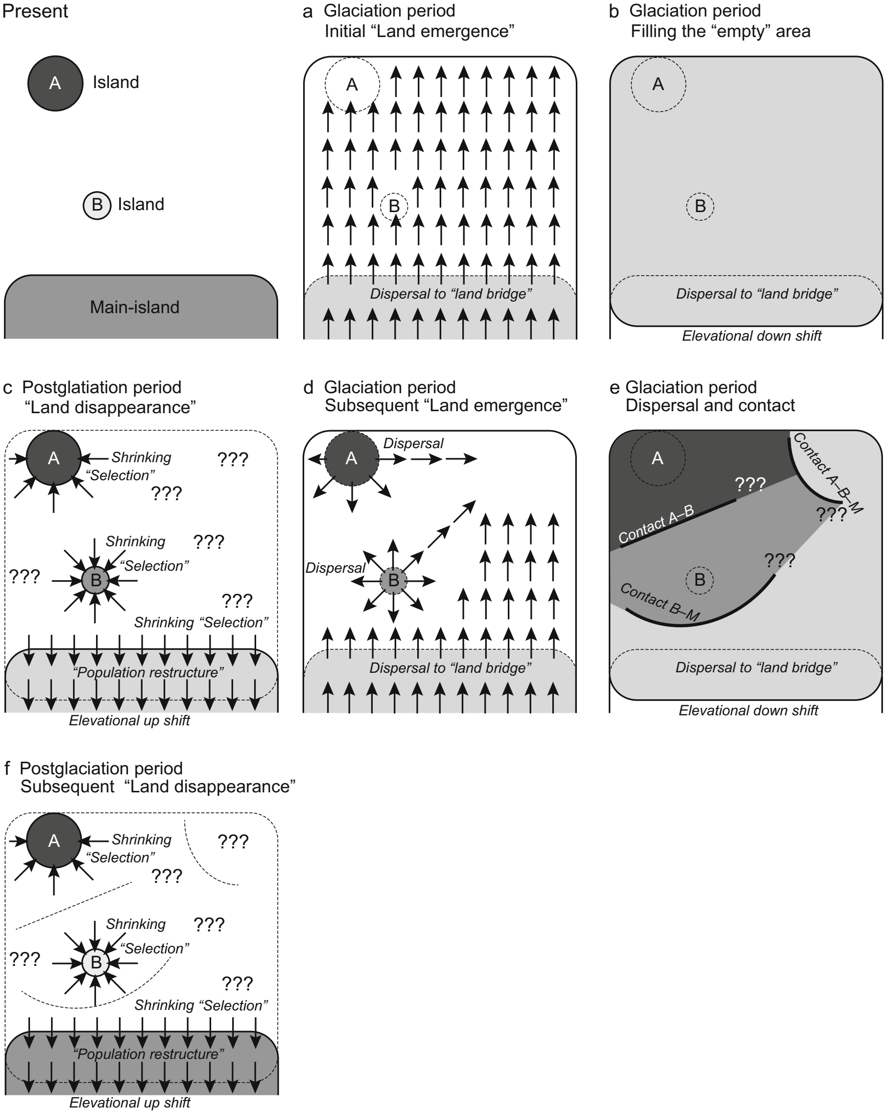

Fig. 1.5 Model for 'land emergence' effect during the repeated glaciation and post-glaciation periods in the Pleistocene (**a**–**f**) to the present (*upper left*). *Shaded areas* indicate the existence of the animal populations using *different colors* for morphological and genetic differentiations. *Solid lines* and *arrows* indicate the configurations of land areas and the expansion and contraction of the animal populations. (See text for explanation)

When the land formation was repeated in the subsequent glaciation period during the Pleistocene, and the animal populations already existed in the small islands (A, B), land emergence may have caused more complicated events

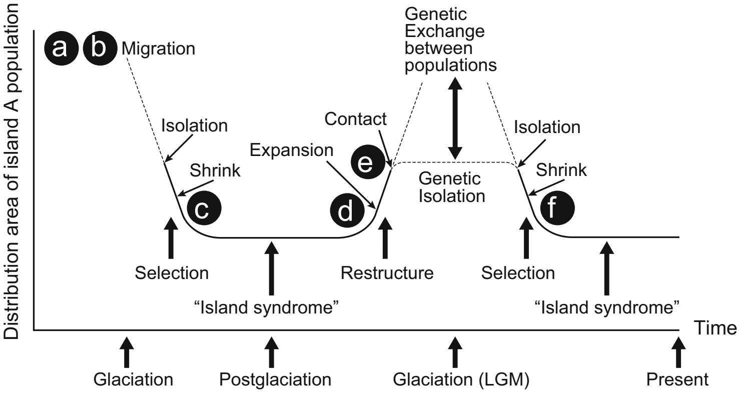

Fig. 1.6 Distribution area changes and expected effects of the adjacent island A population during the repeated glaciation and post-glaciation periods in the Pleistocene. *Letters* **a**–**f** correspond to the events in Fig. 1.5

(Fig. 1.5d). In the glaciation period, once land emergence reoccurred and connected the adjacent islands (A, B) and main islands, animals must have expanded their distribution from island A, island B, and the main island (Fig. 1.5d). With time, dispersed animals from each population made contact with other populations (Fig. 1.5e). It is expected that island population A, island population B, and the main island population could have interbred and genetic structure could have changed, if such populations had not diverged and had not completed pre-mating or post-mating reproductive isolation. On the other hand, if such populations had complete reproductive isolation mechanism, the genetic exchange could not occur.

In the period following post-glaciation (Fig. 1.5f), the land emergence area had shrunk, and through contraction of the populations, selection pressures were likely similar to the previous post-glaciation period. Populations of the main island and adjacent islands had split and become isolated, and population restructuring was expected to have occurred in the main island populations together with expansion resulting from an elevation up-shift. In these glaciation–post-glaciation periods, the population expansions and contractions (Fig. 1.5e, f) were expected to become more complicated than the initial formation of adjacent island populations (Fig. 1.5b, c), because the already-diverged or heterogeneous populations were involved, and interbreeding should be considered as secondary contact and admixture of the concerned populations. Reflecting the degree of admixture and differential response to contraction, the newly formed populations of the adjacent islands and the main island could have experienced drastic change or even complete replacement of morphological and genetic characteristics (shown as different colors for island B and the main island in Fig. 1.5c, f), but they also may remain unchanged (as in island A, in spite of the land connection with island B and the main island). In *A. speciosus*, some adjacent island populations that showed high morphological and genetic divergence from the main island population also showed potential subsequent nuclear gene exchange with the main island populations (Tomozawa and

Suzuki 2008). Such genetic exchanges might be better explained by the land emergence effect, and future studies should be conducted using well-designed samples.

Based on the land emergence effect (Fig. 1.5a–f), I postulate that the land emergence and its disappearance during the repeated glaciation and post-glaciation periods caused complicated population events in the adjacent islands as well as on the main island. The changes in land area of adjacent island populations are summarized in Fig. 1.6, and the corresponding events are as already mentioned. In addition, the so-called island syndrome during the complete isolation of an island is also an important factor that can add complexity to adjacent island populations. Motokawa (2014) suggested that responses to expansion and contraction that differ between sexes and even among populations are caused by variation in ecological and sociological backgrounds and differential responses to land emergence. Motokawa (2014) discussed the example of a shrew, *Crocidura shantungensis*, that established geographic variation in the islands between Tsushima Island, Japan, Jeju Island, Korea, and Taiwan, and also exhibited different extents of sexual dimorphism among the three islands (Motokawa et al. 2003), but the ecological features of this species have not been studied.

Previous phylogeographic data should be reconsidered for each species based on this new idea, incorporating the species-specific parameters especially for dispersal, sociality, habitat, life history, and locomotive ability; in addition to the present and past geomorphological and climate characters and their changes. Incongruent patterns of mitochondrial and nuclear gene phylogeography may become the key to understanding expansion and contraction events resulting from the increase and decrease of land emergence during the repeated glaciation and post-glaciation periods of the Pleistocene.

1.4 'Elevation Shift' Effect

High mountains are considered to function as geographic barriers and produce geographic isolation. This isolation has been well discussed for populations distributed in higher elevations that can be split and isolated as so-called sky islands. However, such distributions are thought to have changed during the Quaternary period, reflecting the climate changes in glaciation and post-glaciation periods: down-shift in the glacial period and up-shift in the post-glaciation period in general. This model is, however, incomplete because it neglects the geomorphological limitations. In an area with complicated geomorphology, elevation distribution shifts may produce and collapse the dispersal barriers, and the actual figures should be analyzed using the potential distribution model. Galbreath et al. (2009) proposed the importance of elevation shifts for montane species, whereas this chapter, based on Shintaku and Motokawa (2016), focuses on the importance of elevation shifts in low elevation species.

Motokawa (2008) showed the potential distribution for the common lowland species of field mouse, *Apodemus speciosus*, based on elevation less than 1000 m. The species is thought to be distributed everywhere over the Japanese Islands, but the potential distribution showed that the uninhabited areas expanded in central Honshu within the mountainous region. The populations in eastern and western Honshu may be connected with narrow corridors on the coast of the Pacific exposure and the very narrow coastal areas on the Sea of Japan side, as well as Ina Valley from southwest to northeast of the mountains, forming a valley of about 600 m elevation among mountains higher than 1000 m.

Shintaku and Motokawa (2016) expanded the idea to estimate the potential distribution in the glaciation period for *A. speciosus*. Currently, in central Honshu (Fig. 1.4c), it is clear that the mountain masses form geological barriers for dispersal between the western and eastern parts, whereas the eastern and western populations are connected by passageways or corridors on the Pacific Ocean coast, the Sea of Japan coast, and Ina Valley. Contrastingly, in the LGM (Fig. 1.4d), the potential distribution (indicated by white) was completely separated between the west and the east by the presence of a mountain mass in the central part of Honshu (shown in black). Eastern and western populations had been further isolated and fragmented by the occurrence of the mountains. These two potential distributions in the present and in the LGM suggest that the within-island geographic barriers and corridors could exist only through elevation distribution and elevation shift in response to the climate change during the repeated glaciation and post-glaciation periods in the Pleistocene. Such ‘cryptic barriers’ or ‘cryptic corridors’ are expected to have dynamically changed in response to the elevation shift of the species. In some cases they appeared only in the transitional short period during the distribution shift, and likely contributed significantly to formation of the complicated patterns of within-island diversification. For several species with a similar history of migration to Japanese islands, slight differences in elevation distribution may have resulted in completely different patterns of within-island diversification. On the other hand, dynamic distribution changes, by using cryptic barriers and cryptic corridors, may have erased or changed the previous structure of within-island diversification.

This model could provide the clue to elucidate the phylogeographic histories of *A. speciosus*, which has complicated divergence patterns in the main Japanese islands: different chromosome numbers in eastern and western populations with a hybrid zone in central Honshu (around Ina Valley) (Tsuchiya et al. 1973; Tsuchiya 1974), no significant geographic divergence but high variability on the main Japanese islands in mitochondrial cytochrome *b* gene haplotypes (Suzuki et al. 2004; Tomozawa and Suzuki 2008), and complex external/cranial morphology (Kobayashi 1981; Kageyama et al. 2009; Shintaku et al. 2012; Shintaku and Motokawa 2016). Cryptic barriers or corridors are expected to have had a role in producing bottleneck or drift effects and in sudden changes in the genetic and morphological structure of this region’s population.

In this chapter, I also want to expand this altitudinal distribution change effect for phylogenetically related, co-occurring species. *Apodemus argenteus* is

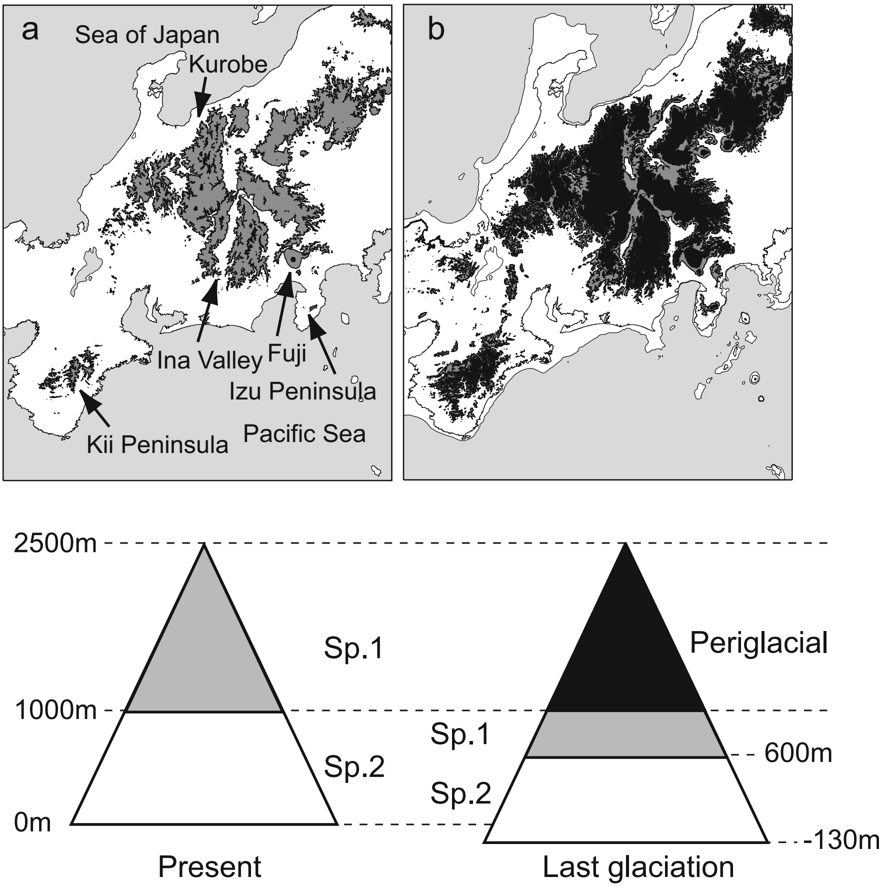

Fig. 1.7 'Elevation shift' in the central part of Japan involving two murid species (*Apodemus speciosus* and *Apodemus argenteus*, as examples for lower and higher elevation species, respectively). (**a**) Current potential distribution of the lower species (*white*, 0–1000 m) and higher species (*gray*, 1000–2500 m). (**b**) Estimated potential distribution in LGM of the lower species (*white*, −130 to 600 m) and higher species (*gray*, 600 to 1000 m)

congeneric with *A. speciosus*; it is smaller than the latter and more adapted to higher elevation and forest habitats. These two species currently overlap in distribution, but their elevation ranges are slightly different. Omitting the overlapping elevations to simplify the model, I set up the current main distribution elevation of *A. speciosus* as 0–1000 m, and higher species (*A. argenteus*) to be 1000–2500 m (Fig. 1.7a). In LGM, the *A. speciosus* main distribution was less than 500 m (half of the current main distribution, instead of 600 m as in Shintaku and Motokawa 2016), but the maximum potential elevation of *A. argenteus* was 1000 m. This design is based on the fact that the periglacial region is thought to have existed at more than

1000 m in central Honshu (Ono 1991) and to be not suitable for the distribution of this animal (Fig. 1.7b).

Interestingly different patterns were found for the two species. The lower species (*A. speciosus*) was continuously distributed in the present, whereas it was very fragmented in the LGM, as predicted earlier. As well, the high altitude species (*A. argenteus*) currently has several isolated distribution ranges, whereas those areas might have been more fragmented during the LGM.

This elevation shift effect is, of course, not limited to *Apodemus* mice. It can be applied and tested for many terrestrial animal species with various preferences and parameters for elevation distribution, as well as habitat selection and dispersal ability. Considering the diversity of loading capacities of related animal species, interaction with ecologically related species that have different but overlapping elevation ranges should be studied for better understanding of the development of species diversity of the animals in Japan.

1.5 Conclusion

The refugia theory is often emphasized in recent molecular phylogeographic studies (Avise 2000), but my “elevation shift” effect may suggest that animal distribution changes had not been as simple as in the application of refugia theory, as a consequence of the complicated geomorphology in mountain regions such as the main Japanese islands. In this case, the animals could seek suitable habitat with limitation of dispersal in connected distribution areas. Dynamic distribution changes in Honshu have been suggested for several animal species (Kawamoto et al. 2007; Oshida et al. 2009), and the elevation shift is proposed to be an important factor for divergence also in Taiwan animals (Yuan et al. 2006; Oshida et al. 2011), but the idea of connectivity in consideration of the cryptic barriers and cryptic corridors has not yet been discussed. The refugia theory has often been used to postulate that the favorable or suitable habitat in the LGM was refugia. I suggest that the actual refugia in LGM should not always be the favorable places, but rather that it could be the better or suitable places with potential survivability under the strongly limited connectivity resulting from temporal and cryptic barriers and corridors.

In this chapter, I discussed new models for animal distribution change as land emergence and elevation shift effects in the repeated glaciation and post-glaciation periods for the development of current diversification among the populations of the main islands and adjacent islands. In *A. speciosus*, currently available morphological and genetic data still indicate different divergence patterns that have not been well interpreted. These two new hypotheses are expected to explain this complicated story. Both effects superficially appear to be independent events, but they are actually related to each other and inseparable. Animal distributions change with elevation, and on the surface, in response to area availability, and connectivity (land emergence or cryptic corridors) or geological and biological isolation between populations must be considered. Complicated geomorphology and geological changes should be carefully considered, together with the factors related to climate response and animal distribution changes in the species concerned. The latter is species specific and includes dispersal, sociality, habitat, life history, and locomotive ability. Interspecific interaction may also be involved. Therefore, we need to reconstruct the potential distribution in the present and in the past in each area and for each species with careful consideration of species-specific parameters. Extinction of animals during the Pleistocene, including LGM, has been interpreted in terms mainly of human impact (Kawamura 2007; Kawamura and Nakagawa 2012), but it can be reconsidered with my model for better understanding.

The two new models might be not limited to island divergence, but could also be applicable to continental divergence and to projections of response to future climate change. These hypotheses are expected to be tested and improved using various species in the Japanese Islands and the continent. For the next steps, two alternative concepts of 'continent' and 'island' and their boundaries should be carefully reconsidered to improve understanding of the biogeography of animals in Asia, including Japan. Understanding the species diversity of animals in Japan will contribute much to biogeography globally.

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References

Abe H (1999) Diversity and conservation of mammals of Japan. In: Yokohata Y, Nakamura S (eds) Recent advances in the biology of Japanese Insectivora. Hiba Society of Natural History, Shobara, pp 89–104

Adler GH, Levins R (1994) The island syndrome in rodent populations. Q Rev Biol 69:473–490

Avise JC (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge

Darlington PJ Jr (1957) Zoogeography: the geographic distribution of animals. Wiley, New York

Dobson M (1994) Patterns of distribution in Japanese land mammals. Mamm Rev 24:91–111

Dobson M, Kawamura Y (1998) Origin of the Japanese land mammal fauna: allocation of extant species to historically-based categories. Quat Res Tokyo 37:385–395

Galbreath KE, Hafner DJ, Zamudio KR (2009) When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). Evolution 63:2848–2863

Hikida T (2002) Natural history of the reptiles. University of Tokyo Press, Tokyo [in Japanese]

Hikida T (2003) Biogeography of reptiles in islands in East Asia—geographic distributions from views of molecular and morphological studies. Seibutsu Kagaku 54:205–220

Hikida T, Motokawa J (1999) Phylogeographical relationships of the skinks of the genus *Eumeces* (Reptilia: Scincidae) in East Asia. In: Ota H (ed) Tropical island herpetofauna: origin, current diversity, and conservation. Elsevier Science, Amsterdam, pp 231–247

Hikida T, Ota H (1997) Biogeography of reptiles in the subtropical East Asian islands. In: Lue KY, Chen TH (eds) Proceedings of the symposium on the phylogeny, biogeography and conservation of fauna and flora of East Asian region. National Science Council, Taipei, pp 11–28

Hikida T, Ota H, Toyama M (1992) Herpetofauna of an encounter zone of Oriental and Palearctic elements: amphibians and reptiles of the Tokara Group and adjacent islands in the northern Ryukyus, Japan. Biol Mag Okinawa 30:29–43

Kageyama M, Motokawa M, Hikida T (2009) Geographic variation in morphological traits of the large Japanese field mouse, *Apodemus speciosus* (Rodentia, Muridae), from the Izu Island Group, Japan. Zool Sci 26:266–276

Kawamoto Y, Shotake T, Nozawa K, Kawamoto S, Tomari K, Kawai S, Shirai K, Morimitsu Y, Takagi N, Akaza H, Fujii H, Hagihara K, Aizawa K, Akachi S, Oi T, Hayaishi S (2007) Postglacial population expansion of Japanese macaques (*Macaca fuscata*) inferred from mitochondrial DNA phylogeography. Primates 48:27–40

Kawamura Y (2007) Last glacial and Holocene land mammals of the Japanese Islands: their fauna, extinction and immigration. Quat Res (Tokyo) 46:171–177

Kawamura Y, Nakagawa R (2012) Terrestrial mammal faunas in the Japanese Islands during OIS 3 and OIS 2. In: Ono A, Izuho M (eds) Environmental changes and human occupation in East Asia during OIS 3 and OIS 2. Archaopress, Oxford, pp 33–54

Kimura M (1996) Quaternary paleogeography of the Ryukyu Arc. J Geogr 105:259–285 [in Japanese with English abstract]

Kizaki K, Oshiro I (1977) Paleogeography of the Ryukyu Islands. Mar Sci Mon 9:542–549 [in Japanese with English abstract]

Kizaki K, Oshiro I (1980) The origin of the Ryukyu Islands. In: Kizaki K (ed) Natural history of the Ryukyus. Tsukiji Shokan, Tokyo, pp 8–37 [in Japanese]

Kobayashi T (1981) On the reliable using of scientific names of the Japanese field mice, *Apodemus*. Honyurui Kagaku (Mamm Sci) 42:27–33 [in Japanese]

Kuroda N (1931) Evaluation of the Watase's line from the view point of vertebrate distribution. Zool Mag (Tokyo) 43:172–175 [in Japanese]

Lomolino MV (2005) Body size evolution in insular vertebrates: generality of the island rule. J Biogeogr 32:1683–1699

Lomolino MV, Sax DF, Palombo MR, van der Geer AA (2012) Of mice and mammoths: evaluations of crucial explanations for body size evolution in insular mammals. J Biogeogr 39:842–854

Lomolino MV, van der Geer AA, Liras GA, Palombo MR, Sax DF, Rossi R (2013) Of mice and mammoths: generality and antiquity of the island rule. J Biogeogr 40:1427–1439

Meiri S, Cooper N, Purvis A (2008) The island rule: made to be broken? Proc R Soc B Biol Sci 275:141–148

Millien-Parra V, Jaeger JJ (1999) Island biogeography of the Japanese terrestrial mammal assemblages: an example of a relict fauna. J Biogeogr 26:959–972

Motokawa M (2000) Biogeography of living mammals in the Ryukyu Islands. Tropics 10:63–71

Motokawa M (2008) Small mammals of Japan, from the viewpoint of zoogeography. In: Motokawa M (ed) Mammalogy in Japan 1, small-sized mammals. University of Tokyo Press, Tokyo, pp 1–29 [in Japanese]

Motokawa M (2009) Distribution patterns and zoogeography of Japanese mammals. In: Ohdachi SD, Ishibashi Y, Iwasa MA, Saitoh T (eds) The wild mammals of Japan. Shoukadoh Book Sellers, Kyoto, pp 44–46

Motokawa M (2014) "Island rule" as viewed from small mammals of Japan: discussion and prospect with emphasis on the Japanese large field mouse. Seibutsu Kagaku 66:4–14 [in Japanese]

Motokawa M (2015) Distribution patterns and zoogeography of Japanese mammals. In: Ohdachi SD, Ishibashi Y, Iwasa MA, Fukui D, Saitoh T (eds) The wild mammals of Japan. Shoukadoh Book Sellers, Kyoto, pp 44–46

Motokawa M, Lin LK, Harada M, Hattori S (2003) Morphometric geographic variation in the Asian lesser white-toothed shrew *Crocidura shantungensis* (Mammalia, Insectivora) in East Asia. Zool Sci 20:789–795

Ohshima K (1990) The history of straits around the Japanese Islands in the late-Quaternary. Quat Res (Tokyo) 29:193–208 [in Japanese with English abstract]

Ohshima K (1991) The late-Quaternary sea-level change of the Japanese Islands. J Geogr 100: 967–975 [in Japanese]

Ono Y (1991) Glacial and periglacial paleoenvironments in the Japanese Islands. Quat Res (Tokyo) 30:203–211

Oshida T, Masuda R, Ikeda K (2009) Phylogeography of the Japanese giant flying squirrel, *Petaurista leucogenys* (Rodentia: Sciuridae): implication of glacial refugia in an arboreal small mammal in the Japanese Islands. Biol J Linn Soc 98:47–60

Oshida T, Lin LK, Chang SW, Chen YJ, Lin JK (2011) Phylogeography of two sympatric giant flying squirrel subspecies, *Petaurista alborufus lena* and *P. philippensis grandis* (Rodentia: Sciuridae), in Taiwan. Biol J Linn Soc 102:404–419

Osozawa S, Shinjo R, Armid A, Watanabe Y, Horiguchi T, Wakabayashi J (2012) Paleogeographic reconstruction of the 1.55 Ma synchronous isolation of the Ryukyu Islands, Japan, and Taiwan and inflow of the Kuroshio warm current. Int Geol Rev 54:1369–1388

Osozawa S, Su ZH, Oba Y, Yagi T, Watanabe Y, Wakabayashi J (2013) Vicariant speciation due to 1.55 Ma isolation of the Ryukyu Islands, Japan, based on geological and GenBank data. Entomol Sci 16:267–277

Osozawa S, Takahashi M, Wakabayashi J (2015) Ryukyu endemic *Mycalesis* butterflies, speciated vicariantly due to isolation of the islands since 1.55 Ma. Lepidoptera Sci 66:8–14

Ota H (1998) Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Res Popul Ecol 40:189–204

Ota H (2000) The current geographic faunal pattern of reptiles and amphibians of the Ryukyu Archipelago and adjacent regions. Tropics 10:51–62

Ota H, Sakaguchi N, Ikehara S, Hikida T (1993) The herpetofauna of the Senkaku Group, Ryukyu Archipelago. Pac Sci 47:248–255

Ota Y, Koike K, Chinzei K, Nogami M, Machida H, Matsuda T (2010) Geomorphology of the Japanese islands. University of Tokyo Press, Tokyo [in Japanese]

Sato JJ (2016) A review of the processes of mammalian faunal assembly in Japan: insights from molecular phylogenetics. In: Motokawa M, Kajihara H (eds) Species diversity of animals in Japan. Springer Japan, Tokyo, pp 49–116

Shintaku Y, Motokawa M (2016) Geographic variation in skull morphology of the large Japanese field mice, *Apodemus speciosus* (Rodentia: Muridae) revealed by geometric morphometric analysis. Zool Sci 32:132–145

Shintaku Y, Kageyama M, Motokawa M (2012) Morphological variation in external traits of the large Japanese field mouse, *Apodemus speciosus*. Mamm Stud 37:113–126

Suzuki H, Yasuda SP, Sakaizumi M, Wakana S, Motokawa M, Tsuchiya K (2004) Differential geographic patterns of mitochondrial DNA variation in two sympatric species of Japanese wood mice, *Apodemus speciosus* and *A. argenteus*. Genes Genet Syst 79:165–176

Tojo K, Sekiné K, Suzuki T, Saito R, Takenaka M (2016) The species and genetic diversities of insects in Japan, with special reference to the aquatic insects. In: Motokawa M, Kajihara H (eds) Species diversity of animals in Japan. Springer Japan, Tokyo, pp 229–247

Tokuda M (1941a) Nippon seibutsu chiri [Biogeography of Japan]. Kokon Shoin, Tokyo [in Japanese]

Tokuda M (1941b) A revised monograph of the Japanese and Manchou–Korean Muridae. Biogeographica 4:1–155

Tomozawa M, Suzuki H (2008) A trend of central versus peripheral structuring in mitochondrial and nuclear gene sequences of the Japanese wood mouse, *Apodemus speciosus*. Zool Sci 25: 273–285

Tsuchiya K (1974) Cytological and biochemical studies of *Apodemus speciosus* group in Japan. J Mamm Soc Jpn 6:67–87 [in Japanese with English abstract]

Tsuchiya K, Moriwaki K, Yosida TH (1973) Cytological survey in wild population of Japanese wood mouse, *Apodemus speciosus* and its breeding. Exp Anim 22(Suppl):221–229

Whittaker RJ (1998) Island biogeography: ecology, evolution, and conservation. Oxford University Press, Oxford

Yuan SL, Lin LK, Oshida T (2006) Phylogeography of the mole-shrew (*Anourosorex yamashinai*) in Taiwan: implications of interglacial refugia in a high-elevation small mammal. Mol Ecol 15:2119–2130

Chapter 2
An Overview of Recent Marine Biodiversity Research in Japan

Hiroshi Kajihara and Keiichi Kakui

Abstract We review recent activities pertaining to taxonomic studies of marine animals, mostly invertebrates, in Japanese waters. Frequent field workshops have increased our knowledge of local faunas. Minute animals, such as those living in the interstices of sediment particles, are still only fragmentarily known in Japan. Training and research vessels have produced significant results in terms of ocean biology; the invention of the 'inner net' has enabled trawls to catch small-bodied benthos. Deep-sea surveys with submersibles have enabled the collection—and even in situ observation—of gelatinous or fragile animals that were previously difficult or impossible to study. New records for Japan of higher taxa, such as the orders Bochusacea (Crustacea: Malacostraca) and Thermosbaenacea (Crustacea: Malacostraca), the class Monoplacophora (Mollusca), and the phylum Gnathostomulida, clearly show that knowledge of Japan's marine biodiversity remains incomplete. Repeated, long-term surveys should be conducted in both shallow and deep waters.

Keywords Pacific • Sea of Japan • Sagami Bay • East Asia • Interstitial fauna • Meiobenthos • DSV • ROV • AUV

2.1 Introduction

Living in an island country surrounded by the sea, Japanese people have probably been familiar with marine organisms since ancient times, but their view of aquatic animals remained fairly irregular before the eighteenth century (Nishimura 1992a). Until then, species were seldom precisely recognized, except for those that were either highly unusual or were utilized in everyday life, particularly as food (Isono 2006). For instance, most of the marine animals in Nakamura's (1666) illustrated encyclopaedia were identified with collective terms, such as 'jellyfish,' 'octopus,' and 'shrimp,' although a few illustrations correctly depicted particular species, for example, the Japanese horseshoe crab *Tachypleus tridentatus* (Leach, 1819)

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(Japanese name: kabuto-gani) and the Japanese blue crab *Portunus trituberculatus* (Miers, 1876) (Japanese name: gazami).

After Nakamura's era, more than a century elapsed before animals were recorded scientifically in the same way as today. The Dutch medical doctor Maarten Houttuyn (1720–1798) was the first naturalist to report Japanese marine animals using Linnaean nomenclature (Nishimura 1992a). Based on specimens collected by the Swedish naturalist Carl Peter Thunberg (1743–1828) during his stay in Nagasaki in 1775–1776, Houttuyn (1782) reported 36 (including 22 new) species of fish, 4 species of crustaceans, and 2 species of cephalopods. Yet another century passed before Japanese zoologists began to describe marine animals.

The year 1890 can be regarded as the beginning of marine biodiversity research by Japanese scientists. Asajiro Oka (1868–1944) was the first to publish taxonomic descriptions of extant marine animals from Japanese waters, with accounts of the colonial entoproct *Ascopodaria misakiensis* Oka, 1890, which, however, is now regarded as a junior synonym of *Barentsia discreta* (Busk, 1886) (Japanese name: suzu-kokemushi) (T. Iseto, personal communication). Three months earlier than Oka's (1890) paper, the palaeontologist Matajiro Yokoyama (1860–1942) reported 62 species among fossils from Hokkaido, describing 36 species as new to science (10 bivalves, 5 gastropods, 7 cephalopods, and 14 foraminiferans) (Yokoyama 1890). The earliest valid species name for a living marine animal published by a Japanese scientist is that of the edible jellyfish *Rhopilema esculenta* Kishinouye (1891) (Japanese name: bizen-kurage), with the description and figures appearing 1 year earlier (Kishinouye 1890) than the Linnaean binomen (Kishinouye 1891).

The following three points are worth noting in terms of substantial contributions toward the development of marine zoosystematics in Japan after 1890, although space limitation precludes going into detail. (1) Numerous publications in Japanese helped beginners to learn animal diversity, for example, textbooks such as *A Manual of Zoology* (Ijima 1918), the 10-volume treatise *Systematic Zoology* (Tokioka et al. 1961; Kuroda 1962; Uchida and Yagyu 1962; Kuroda and Remane 1963; Matsubara 1963; Uchida and Matsubara 1963; Shiino 1964; Uchida et al. 1965a, b, c, 1966, 1967, 1970, 1974; Utinomi et al. 1966; Ueno et al. 1971; Kuwayama et al. 1972; Ishikawa et al. 1986; Nakamura et al. 1988; Matsui 1992; Iwasawa and Kuramoto 1996, 1997; Okutani et al. 1999; Aoki et al. 2000), and various encyclopaedias (Nishimura 1992a, 1995). (2) SCUBA diving became available in the late 1950s (Harada 1957), revolutionarily expanding subtidal observations and sampling effort. (3) The advent of molecular phylogenetics resulted in the active reclassification of higher taxa (e.g., Kakui et al. 2011). The last field was pioneered in Japan by Hori and Osawa (1987), who used 5S rRNA sequences to try to reconstruct the entire tree of life covering prokaryotes, protistans, plants, fungi, and animals; their analysis included 25 species of marine invertebrates, representing approximately 15 phyla.

From 1890 to the present, many zoologists have been involved in biodiversity research in Japan and surrounding waters, culminating in some ongoing global projects such as the Census of Marine Life (O'Dor 2004; Fujikura et al. 2010). How complete is our knowledge of marine biodiversity around Japan? It is safe to say that research is fairly well advanced for major groups of large-bodied animals, especially those that are commercially important, for which a number of pictorial encyclopaedias—often with detailed identification keys—are available and for which the relevant literature has been compiled. Such volumes exist, for instance, for fish (Nakabo 2013), mollusks (Okutani 2000, 2015), polychaetes (Imajima 1996, 2001, 2007), plankton (Chihara and Murano 1997, covering both phytoplankton and zooplankton), and parasites (Nagasawa et al. 2008, 2013; Nagasawa and Uyeno 2014). According to Fujikura et al. (2010), about 33,600 species of marine organisms had been reported from Japanese waters, whereas the estimated number of the remaining undescribed or unreported species is approximately 155,500, indicating that more than 70 % of Japan's marine biodiversity remains unknown. How are zoologists tackling this vast diversity? In the rest of this chapter, we review recent research activities in the waters around Japan.

2.2 Sagami Bay: The Best-Studied Area in Japan

Sagami Bay (Fig. 2.1) and adjacent waters are undoubtedly the best studied marine area in Japan. In 1875, the British research vessel HMS *Challenger* made one trawl and two dredge hauls in this area, obtaining more than 300 animal specimens representing 116 species, 84 of which were new to science and 16 of which represented new genera (Nishimura 1992b). Starting in the 1930s, Hirohito, the Emperor Showa, surveyed the fauna of Sagami Bay, using as bases of operation the Imperial Villas, first at Hayama and then Suzaki, and collected on the east and west coasts of the bay, respectively; these efforts continued for about 40 years (National Science Museum 2007). Specimens were examined in the Biological Laboratory of the Imperial Household (BLIH, founded in 1928), and the results have appeared as 14 monographs covering major groups of macrobenthos: Opisthobranchia (BLIH 1949, 1955, 1990), Ascidiacea (BLIH 1953), Brachyura (BLIH 1965), 'corals' (BLIH 1968), Mollusca (BLIH 1971), Asteroidea (BLIH 1973), Anomura (BLIH 1978), Suctoria (BLIH 1980), Ophiuroidea (BLIH 1982), Echinoidea (BLIH 1986), Pycnogonida (BLIH 1987), Demospongiae (BLIH 1989), and Hydrozoa, the group on which His Majesty specialized (Hirohito 1988, 1995). Apart from the BLIH monograph series, papers based on the Emperor Showa's collection include those on the enigmatic cephalodiscid *Atubaria heterolopha* (Sato 1936), the rare sessile ctenophore *Lyrocteis imperatoris* (Komai 1941), nemerteans (Iwata 1957), the stomatopod *Quollastria imperialis* (Manning 1965), and polychaetes (Imajima 1997, 2003).

There have been several more recent iterations of Sagami Bay surveys. The National Science Museum (NSM; renamed in April 2007 as the National Museum of Nature and Science, NMNS) conducted a series of surveys (Synthetic Researches on the Natural History of the Japanese Islands, or SRNHJI) from 1967 to 2001 in various regions of Japan (see Sect. 2.4, Coastal Surveys). One of the target regions, Sagami Bay, resulted in 15 papers that included reports of new species in Ascidia

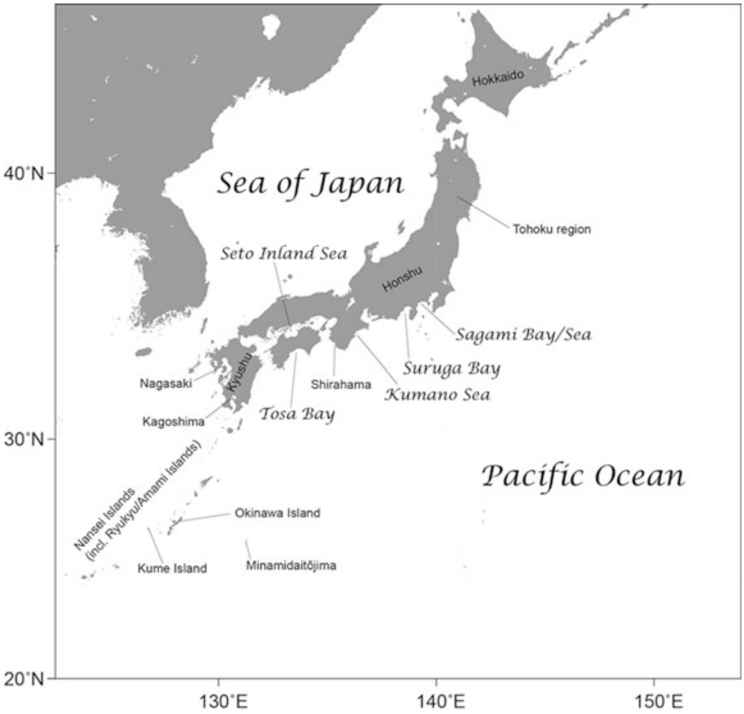

Fig. 2.1 Map of Japan, showing locations for intensive marine biodiversity research (see text for details)

(1 species) (Nishikawa 1982), Mollusca (2 species) (Okutani and Matsukuma 1982), and Porifera (3 species) (Hoshino 1982).

The Japan Agency for Marine–Earth Science and Technology (JAMSTEC) in 1997 investigated the benthopelagic community in Sagami Bay using the manned submersible *Shinkai 2000* (Lindsay et al. 1998) (see Sect. 2.5.3, Surveys with Submersibles).

From 2001 to 2005, NSM conducted an intensive survey entitled "Study on Environmental Changes in the Sagami Sea and Adjacent Coastal Area with Time Serial Comparison of Fauna and Flora," which resulted in three volumes of reports that exceeded 1000 pages in total (NSM 2006a, b, c). A new genus and species of the paralcyoniid octocoral *Nanalcyon sagamiense* Imahara, 2014 was also collected during this survey (Imahara 2014).

In 2009, the Japanese Association for Marine Biology (JAMBIO) was established to accelerate interdisciplinary collaborations among researchers in various fields in marine biology. About 50 potentially undescribed species have been obtained during the six surveys carried out to date (Nakano et al. 2015).

Additional monographs on the Sagami Bay fauna have recently been published on Comatulida (Kogo and Fujita 2014) and Octocorallia (Imahara et al. 2014).

2.3 Meiobenthos

Itô's (1985) handbook of meiobenthos (animals that pass through 1-mm mesh but are retained by 45-μm mesh) for the general public influenced several successive generations of researchers in Japan, but our understanding of the alpha-taxonomy of Japan's meiobenthos remains fragmentary. Littoral meiobenthos described from Japanese coasts since the year 2000 include gnathostomulids (Achatz and Sterrer 2015), gastrotrichs (Chang et al. 2002; Lee and Chang 2011), nemerteans (Kajihara 2007), gastropods (Kano et al. 2003), annelids (Kajihara et al. 2015), kinorhynchs (Murakami et al. 2001; Sørensen et al. 2012; Yamasaki and Kajihara 2012; Yamasaki et al. 2012; Yamasaki and Fujimoto 2014), nematodes (Shimada et al. 2009; Shimada and Kajihara 2014), tardigrades (Fujimoto and Miyazaki 2013; Fujimoto et al. 2013; Fujimoto 2014, 2015a, b), harpacticoids (Song et al. 2012), cyclopoids (Chang 2011), ingolfiellids (Shimomura et al. 2006), and isopods (Shimomura 2005). Ostracods have been much better studied than other taxa (Yamada et al. 2005; Hiruta et al. 2007; Higashi and Tsukagoshi 2008, 2011, 2012; Tanaka and Tsukagoshi 2010, 2013a, b, 2014; Tanaka et al. 2010, 2014; Yamada and Tsukagoshi 2010; Higashi et al. 2011; Yamada and Tanaka 2011, 2013; Dung and Tsukagoshi 2014). Among the meiobenthos, *Austrognatharia orientis* Achatz and Sterrer, 2015 (Fig. 2.3c) is the first named species in the phylum Gnathostomulida reported from Japan; the type locality is Hong Kong, but material from Shirahama (Fig. 2.1) is considered to be conspecific.

2.4 Coastal Surveys

NSM's SRNHJI (1967–2001) resulted in reports of both Recent and fossil fauna and flora, published in 35 volumes of the *Memoirs of the National Science Museum* (vols. 1–33, 37–38), of which 108 papers consider living marine animals ranging from sponges to cetaceans. Seventeen papers in the *Memoirs* established a total of 39 new species, 1 new subspecies, and 2 new genera (Morimoto 1974; Imajima 1976, 1977, 1978, 1979; Takeda 1977, 1985; Uchida 1979; Nishikawa 1980, 1982, 1984, 1986; Hoshino 1982; Okutani and Matsukuma 1982; Machida 1984, 1985; Nunomura 1985). Although most of the 108 papers are based on material from the nearshore and shelf zones, 10 papers (including Machida 1984) discuss animals from deeper bottoms in the slope zone (see Sect. 2.5.2, NMNS).

Individual zoologists have only a limited capacity to process samples in the field and laboratory, with respect to both the number of specimens and the number of different taxa to be handled. In the sea, where virtually all animal phyla occur, this can be a great disadvantage, for an important specimen may be wasted simply because one has no idea how to properly process it. Joint surveys involving specialists on different animal taxa is one solution, as is evident, for example, from the success of SRNHJI, as well as a series of field workshops in Hong Kong

(Morton and Tseng 1982; Morton 1990, 1992). Similar workshops of various sizes have been conducted in Japan, with increasing contributions to our knowledge of local marine life.

A field workshop in 2009 in Ooura Bay, Okinawa Island (Fig. 2.1), was supported financially by the Worldwide Fund for Nature, Japan. More than 500 species of decapods and stomatopods, including at least 39 that appeared to be new to science, were collected from shallow waters including estuaries in a 10-day period (WWF-Japan 2009), demonstrating that the local biodiversity was poorly known even in a familiar, easily accessible inner bay. The same year, another field workshop called "Kumejima 2009" was held on Kume Island (Fig. 2.1) (Naruse et al. 2012), in which 50 experts from seven countries participated in a 2-week survey with dredging (Fig. 2.2a) and SCUBA diving, yielding more than 50 previously undescribed species of fish, crustaceans, and echinoderms; among these was the peracaridan crustacean *Thetispelecaris kumejimensis* Shimomura et al., 2012 (Fig. 2.3a), the first representative of the order Bochusacea from the Pacific (and the sixth member of the order). The Ryukyu Islands (Fig. 2.1) harbor unique environments not found around Honshu, such as the groundwater areas including anchialine caves. From a cave on Minamidaitōjima (Fig. 2.1), the peracaridan *Halosbaena daitoensis* Shimomura and Fujita 2009 (Fig. 2.3b) has been described, representing the first record of the order Thermosbaenacea from Asia (Shimomura and Fujita 2009).

A series of young researchers' self-organized field workshops "Umisawakai" began in 2014 (Fig. 2.2b); these workshops include outreach in which researchers introduce their studies and local biodiversity to the public via lectures and presentations. Some of the results from the last three workshops, involving specialists on Cnidaria, Annelida, Bryozoa, Kinorhyncha, Crustacea, Tardigrada, and Echinodermata, have already been published (Fujimoto 2015a; Uyeno 2015).

An ongoing joint project between Kagoshima University and NMNS is now surveying the entire fish fauna around islands in Kagoshima Prefecture (Fig. 2.1). Hundreds of fish species have been documented from Yakushima (951 species), the Iōjima–Takeshima–Shōwa–Iōjima area (414 species), and Yoronjima (697 species, including 1 new species) (Motomura and Matsuura 2010, 2014; Motomura et al. 2013).

2.5 Deep-Water Surveys

2.5.1 Training and Research Vessels

Long-term, repeated surveys are more important for studying marine benthic habitats than for terrestrial ones. Repeated sampling in exactly the same place, which is not difficult on land, especially with the aid of GPS, is difficult in deep-sea dredging and trawling, where towed gear with an aperture of several tens of

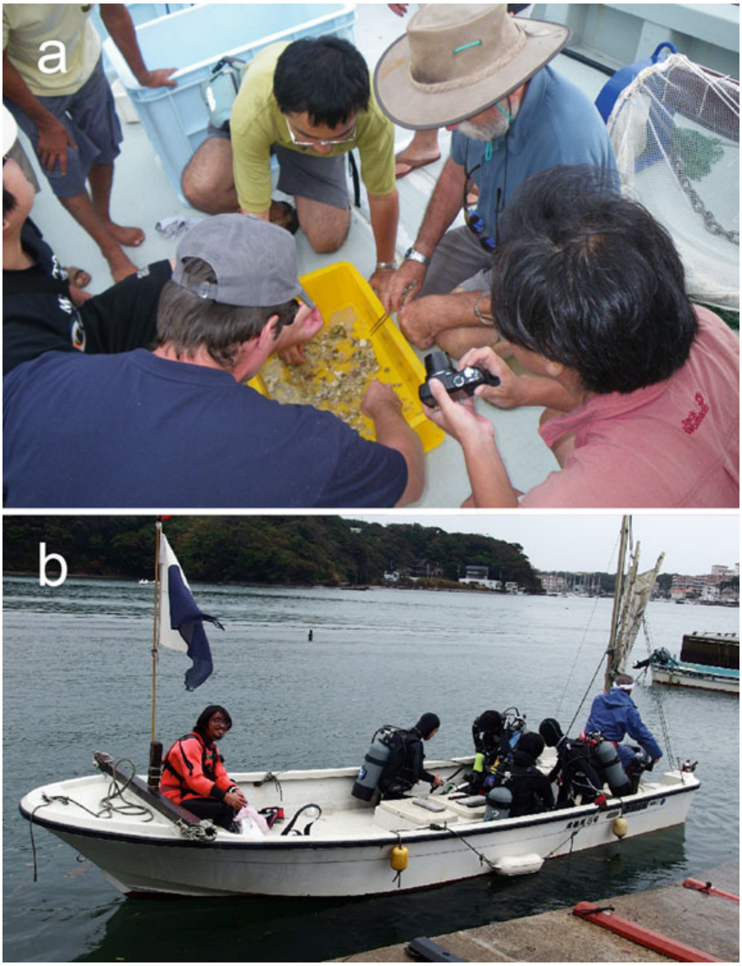

Fig. 2.2 (**a**) Participants in the field workshop “Kumejima 2009” sorting dredged material on board. (**b**) Participants in the field workshop “Umisawakai” held at Misaki Marine Biological Station in 2014, about to depart for SCUBA diving

centimeters or at most a few meters wide is strongly affected by water currents while being lowered hundreds or thousands of meters below the water surface. Simply catching a palm-sized crab dwelling on the sea bottom is highly subject to chance—analogous to catching an apple with a bucket tied to a rope from a balloon 3000 m above the ground. Repetition of sampling is thus crucial for deep-sea benthic inventories.

Remarkable contributions have been made by repeated research cruises by vessels operated by some universities and institutes. Among others, the three training vessels *Toyoshio-maru* (Hiroshima University), *Nagasaki-maru* (Nagasaki

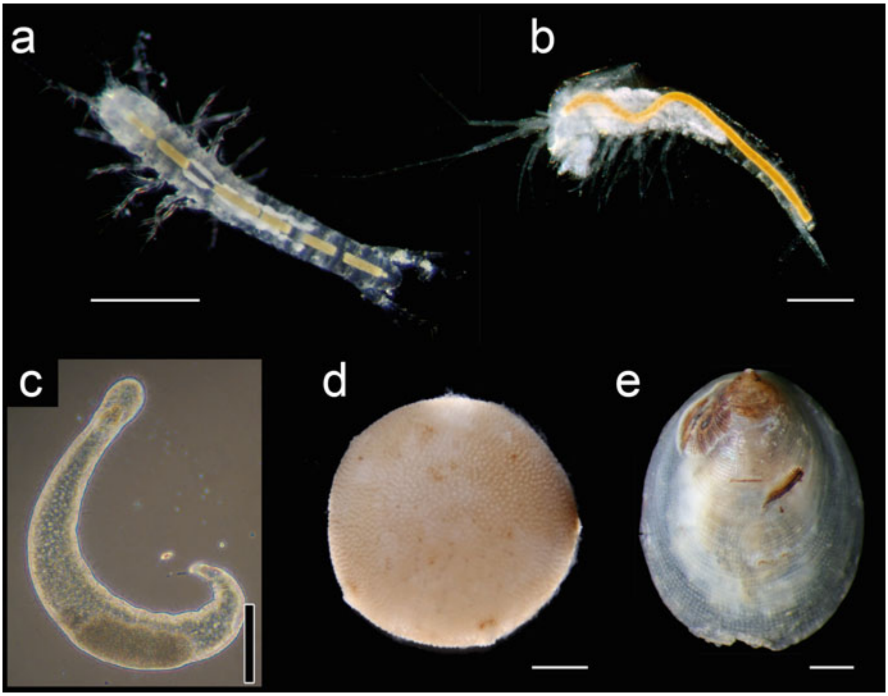

Fig. 2.3 Marine invertebrates belonging to higher taxa that had not been known in Japanese waters before the year 2000. (**a**) *Thetispelacaris kumejimensis* Shimomura et al., 2012 (Crustacea: Bochusacea), fresh specimen. (Photograph © K. Kakui). (**b**) *Halosbaena daitoensis* Shimomura and Fujita, 2009 (Crustacea: Thermosbaenacea). (Photograph courtesy of Y. Fujita; © Y. Fujita). (**c**) *Austrognatharia orientis* Achatz and Sterrer, 2015 (Gnathostomulida). (Creative Commons; after Achatz and Sterrer 2015). (**d**) *Podosphaeraster toyoshiomaruae* Fujita and Rowe, 2002 (Echinodermata: Asteroidea), fresh specimen. (Photograph © K. Kakui). (**e**) *Veleropilina seisuimaruae* Kano et al., 2012 (Mollusca: Monoplacophora). (Photograph courtesy of Y. Kano; © Y. Kano, S. Kimura, T. Kimura, A. Warén, Zoologica Scripta, the Norwegian Academy of Science and Letters; reproduced with permission after Kano et al. 2012). *Bars* (*a*), (*b*), (*e*) 0.5 mm; (*c*) 0.1 mm; (*d*) 2 mm

University), and *Seisui-maru* (Mie University) have yielded significant results with respect to benthic invertebrate systematics.

Since the 1990s, the *Toyoshio-maru* [length overall (LOA), 40.5 m] has conducted surveys in the Seto Inland Sea, the Sea of Japan, and waters around the Nansei Islands (Figs. 2.1, 2.4a), targeting not only benthos but also plankton. These surveys have resulted in discoveries of a number of species new to science or new to Japan, and research reports on decapods (Komatsu and Takeda 2001), sea stars (Fig. 2.3d) (Fujita and Rowe 2002), isopods (Shimomura and Mawatari 2002), fish (Imamura and Shinohara 2003), copepods (Ohtsuka et al. 2003, 2012; Ohtsuka and Boxshall 2004), tanaidaceans (Kakui et al. 2007), nemerteans (Kajihara et al. 2011), and pycnogonids (Takahashi et al. 2012). Among these, Fujita and Rowe (2002) established the new asteroid family Podosphaerasteridae.

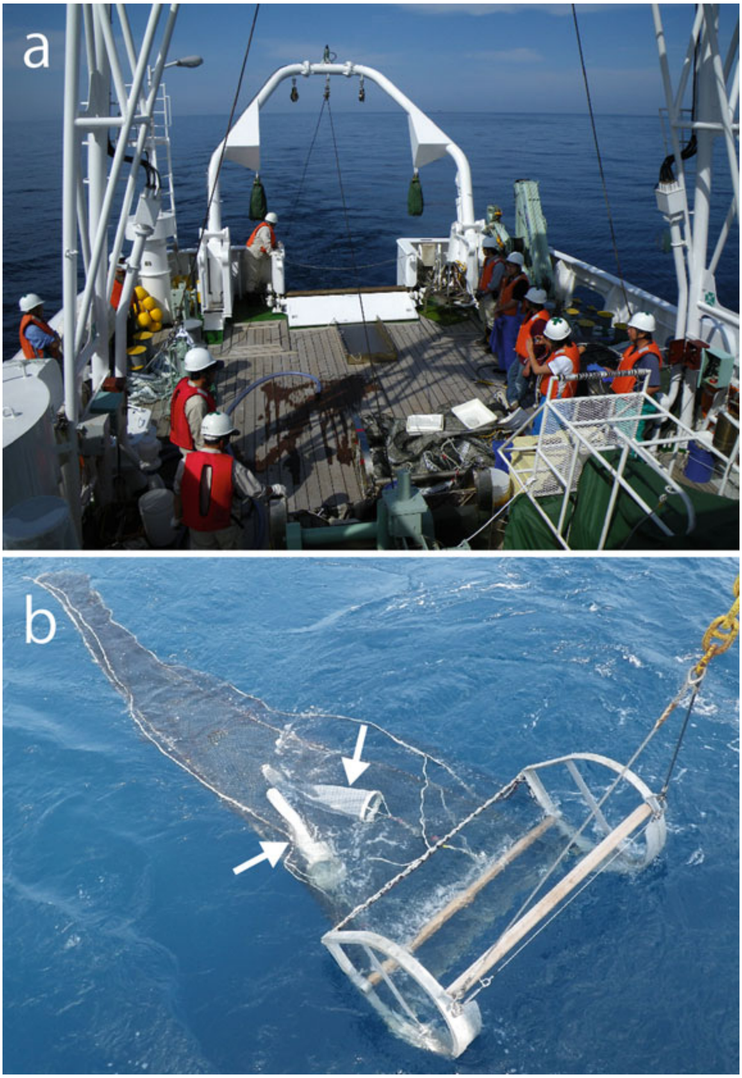

Fig. 2.4 (**a**) Researchers on board the training vessel *Toyoshio-maru*. (**b**) ‘Inner nets’ (*arrows*) set in a trawl

The *Nagasaki-maru* (LOA, 63.87 m) has contributed to marine exploration from west of Kyushu to the Amami Islands. Her cruises were oriented to sampling megabenthos, such as demersal fishes and decapods, before ‘inner nets’ (Fig. 2.4b) were introduced by researchers to capture small crustaceans (Akiyama et al. 2008) and other macrobenthos with body lengths of a few millimetres (Shimomura 2009; Kakui and Kajihara 2011; Akiyama 2012; Shimomura and Kakui 2012).

The *Seisui-maru* (LOA, 50.9 m) has contributed to faunal surveys in Ise Bay and from the Kumano Sea east to the Kii Peninsula (Kimura et al. 2000, 2001; Kano et al. 2012; Izawa 2015). From specimens collected during a cruise for a student field course, Kano et al. (2012) described *Veleropilina seisuimaruae* Kano et al., 2012 (Fig. 2.3e), the first record of the class Monoplacophora (phylum Mollusca) from the Northwest Pacific.

The fisheries research vessel *Soyo-maru* (LOA, 60.0 m) operated by the Fisheries Research Agency, and the research vessels *Hakuho-maru* (LOA, 100 m) and *Shinsei-maru* (LOA, 66 m; successor to the former *Tansei-maru*) of JAMSTEC, have a long history in marine surveys. Published results since 2000 include a monograph on tanaidaceans from the Kurile–Kamchatka and Japan Trenches (Larsen and Shimomura 2007), new species of isopods (Shimomura 2008), a new species of cephalocarid (Shimomura and Akiyama 2008), a new genus of fish (Shinohara and Yabe 2009), a new species of squat lobster (Komai 2011), a new species of brittle star (Okanishi and Fujita 2011), new species of cumaceans (Akiyama and Gerken 2012), a new species of free-living nematode (Shimada et al. 2012), a new species of tanaidacean (Kakui and Yamasaki 2013), and a monograph on polychaetes (Reuscher et al. 2015).

2.5.2 NSM (NMNS)

Although the target depths of NSM's SRNHJI (1967–2001) in terms of living marine animals were mostly in coastal regions (see Sect. 2.4, Coastal Surveys), surveys have also been conducted in deep waters, primarily in the 1980s and 1990s (Machida 1984, 1988; Kubodera 1993, 1996; Takeda 1993; Shinohara et al. 1996; Irimura and Kubodera 1998; Kubodera and Yamada 1998; Takeda and Kubodera 1998).

In 1993, the zoology department of the museum began a series of intensive regional inventories (5 years for each region) of the deep-sea fauna, while at the same time examining the impacts of anthropogenic pollutants on the deep-sea environment. Based on a large number of specimens obtained by dredging from training or research vessels, the results of these surveys have been consecutively published. The first study, conducted in Suruga Bay (NSM 1997) and yielding 20 new species, was followed by projects in Tosa Bay (Fujita et al. 2001), around the Nansei Islands (Hasegawa et al. 2005), off Tohoku (Fujita 2009), and in the Sea of Japan (Fujita 2014) (Fig. 2.1).

2.5.3 Surveys with Submersibles

The inaccessibility of the deep ocean floor has hampered biodiversity research, especially for animals with fragile, soft bodies, or those occupying particular

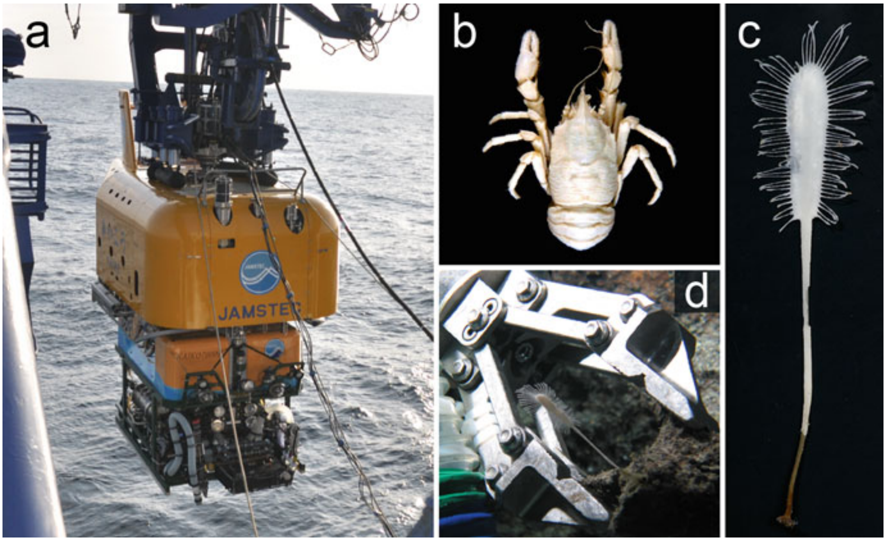

Fig. 2.5 (**a**) The ROV *Kaiko* 7000II of JAMSTEC. (Photograph © K. Kakui). (**b**) *Munidopsis ryukyuensis* Cubelio et al., 2007 (Crustacea: Decapoda) collected near hydrothermal vent by the ROV *Hyper-Dolphin*. (Photograph courtesy of S. Tsuchida; © S. Tsuchida). (**c**) The deep-sea sponge *Abyssocladia natsushimae* Ise and Vacelet, 2010 (Porifera: Demospongiae) collected with the manipulator of the ROV *Hyper-Dolphin* (**d**). (Photograph courtesy of Y. Ise; © Y. Ise, J. Vacelet, Zoological Society of Japan; reproduced with permission after Ise and Vacelet 2010)

habitats such as hydrothermal vents. Only indirect sampling, by means of dredges, trawls, and core samplers, was possible before the invention of manned submersibles (such as the Bathysphere of the American naturalist William Beebe, which came into operation in 1930) permitted visual observations. On the other hand, unmanned submersibles have also been developed in many countries and have led to important biological discoveries, such as hydrothermal vent faunas (Lonsdale 1977) and whale-fall faunas (Smith et al. 1987).

JAMSTEC has played the central role in this field in Japan, conducting surveys with deep-submergence vehicles (DSVs; e.g., *Shinkai* series), remotely operated vehicles (ROVs; e.g., *Hyper-Dolphin*, *Kaiko* series) (Fig. 2.5a), and autonomous underwater vehicles (AUVs; e.g., *Picasso*). Surveys by JAMSTEC have expanded our knowledge of the faunas in specific environments, such as the deep-sea cold-seep clams (Okutani et al. 2004), the decapods around hydrothermal vents (Takeda et al. 2000; Cubelio et al. 2007) (Fig. 2.5b), and the zombie worms (Fujikura et al. 2006) and whale-fall lancelet (Nishikawa 2004) on and around cetacean bones. Dramatic advances have also accrued in research on fragile and/or gelatinous animals, such as comb jellies (e.g., Lindsay 2006; Lindsay and Miyake 2007), bathypelagic ribbonworms (Kajihara and Lindsay 2010), and carnivorous sponges (Ise and Vacelet 2010) (Fig. 2.5c, d).

2.6 Conclusions

As Fujikura et al. (2010) noted, we are only one fifth of the way to a complete understanding of the marine biodiversity in Japanese waters. Discoveries at the level of higher taxa, as exemplified by the crustacean orders Bochusacea (Shimomura et al. 2012) and Thermosbaenacea (Shimomura and Fujita 2009), the molluscan class Monoplacophora (Kano et al. 2012), and the phylum Gnathostomulida (Achatz and Sterrer 2015), indicate that even the framework of our knowledge of Japan's marine life remains incomplete. The success of recent field workshops demonstrates the importance of collaborative research. Repeated surveys of local faunas detect additional unknown animals from all areas—regardless of whether these are areas not previously investigated, or well-studied places such as Sagami Bay, or easily accessible environments such as inner bays. Surveys should be continued in both the deep-sea and the shallow littoral areas.

Means of integrating information need to be developed, given the consensus on the importance of biodiversity conservation. For instance, the website of the Ichthyological Society of Japan (Endo 2015) provides information on fish species (including scientific and Japanese vernacular names, localities, and literature if applicable) that are either new to science or new to Japan since the comprehensive work of Nakabo (2013), and similar systems should be established for other taxa.

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References

Achatz JG, Sterrer W (2015) New Austrognathiidae (Gnathostomulida: Conophoralia) from Hong Kong and Japan: microscopic anatomy, ultrastructure and evolutionary implications. Zootaxa 3955:267–282

Akiyama T (2012) Two new species of *Atlantocuma* (Crustacea: Cumacea), and a new genus and species from Japan, Northwest Pacific, with observations on the degeneration of mouthparts in ovigerous females. Zootaxa 3400:20–42

Akiyama T, Gerken S (2012) The cumacean (Crustacea: Peracarida) genus *Petalosarsia* (Pseudocumatidae) from the Pacific Ocean. Zootaxa 3320:1–35

Akiyama T, Shimomura M, Nakamura K (2008) Collection of deep-sea small arthropods: gears for collection and processing of samples on deck. Taxa 24:27–32 [in Japanese]

Aoki J et al (eds) (2000) Systematic zoology (supplementary edition), Supplementaryth edn. Nakayama-Shoten, Tokyo [in Japanese]

Biological Laboratory, Imperial Household (ed) (1949) Opisthobranchia of Sagami Bay; collected by His Majesty the Emperor of Japan; described, with an introduction, by Kikutaro Baba, D. Sc.; illustrated by Hiroo Sanada and Shiro Kato; edited by Hirotaro Hattori, D.Sc., Chief, Biological Laboratory, Imperial Household. Iwanami Shoten, Tokyo

Biological Laboratory, Imperial Household (ed) (1953) Ascidians of Sagami Bay; collected by His Majesty the Emperor of Japan; described and illustrated by Takasi Tokioka; edited by Hirotaro Hattori, D.Sc., Chief, Biological Laboratory, Imperial Household. Iwanami Shoten, Tokyo

Biological Laboratory, Imperial Household (ed) (1955) Opisthobranchia of Sagami Bay; supplement; collected by His Majesty the Emperor of Japan; described, with an introduction, by Kikutaro Baba, D.Sc.; illustrated by Hiroo Sanada and Shiro Kato; edited by Hirotaro Hattori, D.Sc., Chief, Biological Laboratory, Imperial Household. Iwanami Shoten, Tokyo

Biological Laboratory, Imperial Household (ed) (1965) The crabs of Sagami Bay; collected by His Majesty the Emperor of Japan; described and illustrated by Tune Sakai, D.Sc. Maruzen, Tokyo

Biological Laboratory, Imperial Household (ed) (1968) The hydrocorals and scleractinian corals of Sagami Bay; collected by His Majesty the Emperor of Japan; described by Motoki Eguchi, D.Sc. Maruzen, Tokyo

Biological Laboratory, Imperial Household (ed) (1971) The sea shells of Sagami Bay; collected by His Majesty the Emperor of Japan; described by Tokubei Kuroda, D.Sc., Tadashige Habe, D. Sc., Katura Oyama, D.Sc. Maruzen, Tokyo

Biological Laboratory, Imperial Household (ed) (1973) The sea-stars of Sagami Bay; collected by His Majesty the Emperor of Japan; described by Ryoji Hayashi, D.Sc. Hoikusha, Osaka

Biological Laboratory, Imperial Household (ed) (1978) The crustacean Anomura of Sagami Bay, collected by His Majesty the Emperor of Japan, described by Sadayoshi Miyake, Dr. Agr. Hoikusha, Osaka

Biological Laboratory, Imperial Household (ed) (1980) On the genus *Ephelota* (Ciliophora, Suctoria) from the coasts of Izu Peninsula and Niijima, contributed by Ryozo Yagyu. Hoikusha, Osaka

Biological Laboratory, Imperial Household (ed) (1982) The brittle-stars of Sagami Bay, collected by His Majesty the Emperor of Japan, described by Seiichi Irimura. Maruzen, Tokyo

Biological Laboratory, Imperial Household (ed) (1986) The sea urchins of Sagami Bay, collected by His Majesty the Emperor of Japan, described by Michio Shigei, Dr.Sc. Maruzen, Tokyo

Biological Laboratory, Imperial Household (ed) (1987) The sea spiders of Sagami Bay; collected by His Majesty the Emperor of Japan; described by Koichiro Nakamura. Maruzen, Tokyo

Biological Laboratory, Imperial Household (ed) (1989) The Demospongiae of Sagami Bay, collected by His Majesty the Emperor of Japan, described by Senji Tanita. Biological Laboratory, Imperial Household, Tokyo

Biological Laboratory, Imperial Household (ed) (1990) Opisthobranchia of Sagami Bay; supplement; collected by His Majesty the Emperor of Japan; described, with an introduction, by Kikutaro Baba, D.Sc.; illustrated by Hiroo Sanada and Shiro Kato; revised edition. Iwanami Shoten, Tokyo

Chang C-Y (2011) First record of the genus *Cyclopinoides* (Copepoda, Cyclopoida, Cyclopinidae) from the Pacific. Anim Cells Syst 15:63–72

Chang C-Y, Kubota S, Shirayama Y (2002) New marine gastrotrichs of the family Thaumastodermatidae (Gastrotricha: Macrodasyida) from Shirahama, Japan. Proc Biol Soc Wash 115:769–781

Chihara M, Murano M (eds) (1997) An illustrated guide to marine plankton in Japan. Tokai University Press, Tokyo [in Japanese]

Cubelio SS, Tsuchida S, Watanabe S (2007) New species of *Munidopsis* (Decapoda: Anomura: Galatheidae) from hydrothermal vent in Okinawa Trough and cold seep in Sagami Bay. Crust Res 36:1–14

Dung L-D, Tsukagoshi A (2014) Three new species of the genus *Loxoconcha* (Crustacea, Ostracoda, Podocopida) from the Okinawa Islands, southern Japan. Zootaxa 3796:147–165

Endo H (2015) [List of Japanese fish species not included in Nakabo (2013)]. http://www.fish-isj.jp/info/list_additon.html. Accessed 26 Apr 2015 [in Japanese]

Fujikura K, Fujiwara Y, Kawato M (2006) A new species of *Osedax* (Annelida: Siboglinidae) associated with whale carcasses off Kyushu, Japan. Zool Sci 23:733–740

Fujikura K, Lindsay D, Kitazato H, Nishida S, Shirayama Y (2010) Marine biodiversity in Japanese waters. PLoS ONE 5:e11836

Fujimoto S (2014) A new *Stygarctus* (Arthrotardigrada: Stygarctidae) from Japan, with entangled seminal receptacle ducts. Zootaxa 3784:187–195

Fujimoto S (2015a) Halechiniscidae (Heterotardigrada, Arthrotardigrada) of Oura Bay, Okinawajima, Ryukyu Islands, with descriptions of three new species. ZooKeys 483:149–166

Fujimoto S (2015b) *Quisarctus yasumurai* gen. et sp. nov. (Arthrotardigrada: Halechiniscidae) from a submarine cave, off Iejima, Ryukyu Islands, Japan. Zootaxa 3948:145–150

Fujimoto S, Miyazaki K (2013) *Neostygarctus lovedeluxe* n. sp. from the Miyako Islands, Japan: the first record of Neostygarctidae (Heterotardigrada: Arthrotardigrada) from the Pacific. Zool Sci 30:414–419

Fujimoto S, Miyazaki K, Suzuki AC (2013) A new marine tardigrade, *Tanarctus diplocerus* (Arthrotardigrada: Halechiniscidae), from Japan. J Mar Biol Assoc UK 93:955–961

Fujita T (ed) (2009) Deep-sea fauna and pollutants off Pacific coast of Northern Japan, National Museum of Nature and Science Monographs 39. National Museum of Nature and Science, Tokyo

Fujita T (ed) (2014) Deep-sea fauna of the Sea of Japan, National Museum of Nature and Science Monographs 44. National Museum of Nature and Science, Tokyo

Fujita T, Rowe FWE (2002) Podosphaerasteridae fam. nov. (Echinodermata: Asteroidea: Valvatida), with a new species, *Podosphaeraster toyoshiomaruae*, from southern Japan. Species Divers 7:317–332

Fujita T, Saito H, Takeda M (eds) (2001) Deep-sea fauna and pollutants in Tosa Bay, National Museum of Nature and Science Monographs 20. National Museum of Nature and Science, Tokyo

Harada E (1957) Ecological observations on the Japanese spiny lobster, *Panulirus japonicus* (von Siebold), in its larval and adult life. Publ Seto Mar Biol Lab 6:99–120

Hasegawa K, Shinohara G, Takeda M (eds) (2005) Deep-sea fauna and pollutants in Nansei Islands, National Museum of Nature and Science Monographs 29. National Museum of Nature and Science, Tokyo

Higashi R, Tsukagoshi A (2008) Two new species of *Microloxoconcha* (Crustacea: Ostracoda: Podocopida) from Japan, with a redescription of the genus. Species Divers 13:157–173

Higashi R, Tsukagoshi A (2011) Four new species of the interstitial family Cobanocytheridae (Crustacea: Ostracoda) from central Japan. Zootaxa 2924:33–56

Higashi R, Tsukagoshi A (2012) Two new species of the interstitial genus *Parvocythere* (Crustacea, Ostracoda, Cytheroidea) from Japan: an example of morphological variation. ZooKeys 193:27–48

Higashi R, Tsukagoshi A, Kimura H, Kato K (2011) Male dimorphism in a new interstitial species of the genus *Microloxoconcha* (Podocopida: Ostracoda). J Crust Biol 31:142–152

Hirohito (1988) The hydroids of Sagami Bay; collected by His Majesty the Emperor of Japan. Biological Laboratory, Imperial Household, Tokyo

Hirohito (1995) The hydroids of Sagami Bay II: Thecata; collected by His Majesty the Showa Emperor of Japan; annotated by Mayumi Yamada, Dr.Sc. Professor Emeritus of the Hokkaido University. Biological Laboratory, Imperial Household, Tokyo

Hiruta SF, Hiruta S, Mawatari SF (2007) A new, interstitial species of *Terrestricythere* (Crustacea: Ostracoda) and its microdistribution at Orito Beach, northern Sea of Japan. Hydrobiologia 585: 43–56

Hori H, Osawa S (1987) Origin and evolution of organisms as deduced from 5S ribosomal RNA sequences. Mol Biol Evol 4:445–472

Hoshino T (1982) Description of the dominant species of the class Demospongia dredged from the coastal area of the Izu Peninsula, Sagami Bay. Mem Natl Sci Mus Tokyo 15:139–148, pls 7–8

Houttuyn M (1782) Beschryving van eenige Japanse visschen, en andere zee-schepzelen. Verh Holland Maatsch Wet Haarlem 20:311–350

Ijima I (1918) A manual of zoology. Dainihon-Tosho, Tokyo

Imahara Y (2014) Two new paralcyoniid octocorals from Japan (Anthozoa: Alcyonacea). Zootaxa 3652:424–436

Imahara Y, Iwase F, Namikawa H (2014) The octocorals of Sagami Bay. Tokai University Press, Hadano

Imajima M (1976) Serpulid polychaetes from Tanega-shima, Southwest Japan. Mem Natl Sci Mus Tokyo 9:123–143

Imajima M (1977) Serpulidae (Annelida, Polychaeta) collected around Chichi-jima (Ogasawara Islands). Mem Natl Sci Mus Tokyo 10:89–111

Imajima M (1978) Serpulidae (Annelida, Polychaeta) collected around Nii-jima and Ō-shima, Izu Islands. Mem Natl Sci Mus Tokyo 11:49–72

Imajima M (1979) Serpulidae (Annelida, Polychaeta) collected around Cape Shionomisaki, Kii Peninsula. Mem Natl Sci Mus Tokyo 12:159–183

Imajima M (1996) Kankeidobutsu Tamorui [Annelida Polychaeta]. Seibutsu Kenkyusha, Tokyo [in Japanese]

Imajima M (1997) Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo. Families Polynoidae and Acoetidae. Natl Sci Mus Monogr 13:1–131

Imajima M (2001) Kankeidobutsu Tamorui II [Annelida Polychaeta II]. Seibutsu Kenkyusha, Tokyo [in Japanese]

Imajima M (2003) Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo (II). Orders included within the Phyllodocida, Amphinomida, Spintherida and Eunicida. Natl Sci Mus Monogr 23:1–221

Imajima M (2007) Kankeidobutsu Tamorui III [Annelida Polychaeta III]. Seibutsu Kenkyusha, Tokyo [in Japanese]

Imamura H, Shinohara G (2003) *Cocotropus keramaensis*, a new species of the family Aploactinidae (Teleostei) from the Kerama Islands, southern Japan. Ichthyol Res 50:233–238

Irimura S, Kubodera T (1998) Ophiuroidea in the East China Sea. Mem Natl Sci Mus Tokyo 31: 135–143

Ise Y, Vacelet J (2010) New carnivorous sponges of the genus *Abyssocladia* (Demospongiae, Poecilosclerida, Cladorhizidae) from Myojin Knoll, Izu-Ogasawara Arc, southern Japan. Zool Sci 27:888–894

Ishikawa M, Kawamura K, Taneda Y, Nakauchi M, Nishikawa T, Mukai H, Watanabe H (1986) Systematic zoology, vol 8–3: Hemichordata, Protochordata. Nakayama-Shoten, Tokyo [in Japanese]

Isono N (2006) Old Japanese names of echinoderms. Hiyoshi Rev Nat Sci 39:53–79 [in Japanese]

Itô T (1985) Organisms in sand interstices. Kaimeisha, Tokyo [in Japanese]

Iwasawa H, Kuramoto M (1996) Systematic zoology, vol 9–3: Amphibia (1). Nakayama-Shoten, Tokyo [in Japanese]

Iwasawa H, Kuramoto M (1997) Systematic zoology, vol 9–4: Amphibia (2). Nakayama-Shoten, Tokyo [in Japanese]

Iwata F (1957) Nemerteans from Sagami Bay. Publ Akkeshi Mar Biol Stat 7:1–31

Izawa K (2015) Some new and known species of Hatschekiidae (Copepoda, Siphonostomatoida) parasitic on Japanese actinopterygian fishes belonging to Ophidiiformes, Beryciformes and Scorpaeniformes, with discussion on the female genital system and the insemination mode in Siphonostomatoida. Crustaceana 88:359–384

Kajihara H (2007) *Ototyphlonemertes dolichobasis* sp. nov. (Nemertea: Hoplonemertea: Monostilifera: Ototyphlonemertidae), a new species of interstitial nemertean from Japan. Species Divers 12:57–66

Kajihara H, Lindsay DJ (2010) *Dinonemertes shinkaii* sp. nov. (Nemertea: Hoplonemertea: Polystilifera: Pelagica), a new species of bathypelagic nemertean. Zootaxa 2429:43–51

Kajihara H, Olympia M, Kobayashi N, Katoh T, Chen H-X, Strand M, Sundberg P (2011) Systematics and phylogeny of the hoplonemertean genus *Diplomma* (Nemertea) based on molecular and morphological evidence. Zool J Linn Soc 161:695–722

Kajihara H, Ikoma M, Yamasaki H, Hiruta SF (2015) *Trilobodrilus itoi* sp. nov. and a redescription of *T. nipponicus* (Annelida: Dinophilidae), with a molecular phylogeny of the genus. Zool Sci 32:405–417

Kakui K, Kajihara H (2011) *Pseudosphyrapus cuspidiger* sp. nov. from the Nansei Islands, Japan, with a supplementary description of *Kudinopasternakia balanorostrata* Kakui, Kajihara and Mawatari, 2007 (Crustacea: Tanaidacea: Apseudomorpha: Sphyrapodidae). Bull Natl Mus Nat Sci Ser A Suppl 5:53–70

Kakui K, Yamasaki H (2013) Nototanaids (Crustacea: Tanaidacea) from Japan, with the description of a new species of *Nototanoides*. Species Divers 18:245–254

Kakui K, Kajihara H, Mawatari SF (2007) Two new sphyrapodid species (Crustacea: Tanaidacea: Apseudomorpha) from southwestern Japan. Zootaxa 1563:37–54

Kakui K, Katoh T, Hiruta SF, Kobayashi N, Kajihara H (2011) Molecular systematics of Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of suborder/superfamily-level classification. Zool Sci 28:749–757

Kano Y, Kase T, Kubo H (2003) The unique interstitial habitat of a new neritiliid gastropod, *Neritilia littoralis*. J Mar Biol Assoc UK 83:835–840

Kano Y, Kimura S, Kimura T, Warén A (2012) Living Monoplacophora: morphological conservatism or recent diversification? Zool Scr 41:471–488

Kimura S, Yamashita T, Iwatsuki Y (2000) A new species, *Gazza rhombea*, from the Indo-West Pacific, with a redescription of *G. achlamys* Jordan & Starks, 1917 (Perciformes: Leiognathidae). Ichthyol Res 47:1–12

Kimura S, Iwatsuki Y, Yoshino T (2001) Redescriptions of the Indo-West Pacific atherinid fishes, *Atherinomorus endrachtensis* (Quoy and Gaimard, 1825) and *A. duodecimalis* (Valenciennes *in* Cuvier and Valenciennes, 1835). Ichthyol Res 48:167–177

Kishinouye K (1890) Bizen-kurage. Zool Mag 2:47–54

Kishinouye K (1891) Bizen-kurage [*Rhopilema esculenta*]. Zool Mag 3:53 [in Japanese]

Kogo I, Fujita T (2014) The feather stars of Sagami Bay. Tokai University Press, Hadano [in Japanese]

Komai T (1941) A new remarkable sessile ctenophore. Proc Imp Acad 17:216–220

Komai T (2011) A new species of the squat lobster genus *Munida* (Decapoda: Anomura: Munididae) from the North Pacific off Japan. Bull Natl Mus Nat Sci Ser A Suppl 5:101–108

Komatsu H, Takeda M (2001) On *Merocryptoides*, a leucosiid crab genus (Crustacea: Decapoda: Brachyura) endemic to Japan, with description of two new species. Zool Sci 18:993–1002

Kubodera T (1993) Upper bathyal cephalopods off eastern Cape Erimo, Hokkaido, Japan. Mem Natl Sci Mus Tokyo 26:83–88 [in Japanese with English summary]

Kubodera T (1996) Cephalopod fauna off Sanriku and Joban districts, northeastern Japan. Mem Natl Sci Mus Tokyo 29:187–207

Kubodera T, Yamada H (1998) Cephalopod fauna around the continental shelf of the East China Sea. Mem Natl Sci Mus Tokyo 31:187–210

Kuroda N (1962) Systematic zoology, vol 10–1: Aves. Nakayama-Shoten, Tokyo [in Japanese]

Kuroda N, Remane A (1963) Systematic zoology, vol. 10–2: Mammalia (trans. Uchida T). Nakayama-Shoten, Tokyo [in Japanese]

Kuwayama S, Miyamoto S, Kuroko H, Okada T, Sakaguchi K, Nakane T, Yasumatsu K (1972) Systematic zoology, vol 7–3: Insecta (3). Nakayama-Shoten, Tokyo [in Japanese]

Larsen K, Shimomura M (eds) (2007) Tanaidacea (Crustacea: Peracarida) from Japan. III. The deep trenches; the Kurile-Kamchatka Trench and Japan Trench. Zootaxa 1599:5–12

Lee J, Chang C-Y (2011) Two new species of the genus *Lepidodasys* (Gastrotricha, Lepidodasyidae) from Tsushima Island, Japan. J Nat Hist 45:855–867

Lindsay DJ (2006) A checklist of midwater cnidarians and ctenophores from Sagami Bay: species sampled during submersible surveys from 1993–2004. Bull Plankton Soc Jpn 53:104–110 [in Japanese]

Lindsay DJ, Miyake H (2007) A novel benthopelagic ctenophore from 7,217 m depth in the Ryukyu Trench, Japan, with notes on the taxonomy of deep-sea cydippids. Plankton Benthos Res 2: 98–102

Lindsay DJ, Hunt J, Hashimoto J, Fujikura K, Fujiwara Y, Tsuchida S, Itoh K (1998) The benthopelagic community of Sagami Bay. JAMSTEC J Deep Sea Res 14:493–499 [in Japanese with English abstract]

Lonsdale P (1977) Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. Deep-Sea Res 24:857–863

Machida M (1984) Trematodes of marine fishes from depth of 200–400 m off Yamagata, the Japan Sea. Mem Natl Sci Mus Tokyo 17:101–110

Machida M (1985) A new lissorchiid trematode from zoarcid fish in the Sea of Japan. Mem Natl Sci Mus Tokyo 18:117–120

Machida M (1988) Two species of trematodes from deep-sea fishes of northern Japan. Mem Natl Sci Mus Tokyo 21:107–112

Manning R (1965) Stomatopoda from the collection of His Majesty the Emperor of Japan. Crustaceana 9:249–262

Matsubara K (1963) Systematic zoology, vol 9–2: Pisces (2). Nakayama-Shoten, Tokyo [in Japanese]

Matsui M (1992) Systematic zoology, vol 9–6: Reptilia (2). Nakayama-Shoten, Tokyo [in Japanese]

Morimoto Y (1974) Bathynellid crustaceans from the islands of Okinawa and Ishigaki-jima in the Ryukyus. Mem Natl Sci Mus Tokyo 7:135–143

Morton B (ed) (1990) The marine flora and fauna of Hong Kong and southern China II (three volumes). Hong Kong University Press, Hong Kong

Morton B (ed) (1992) The marine flora and fauna of Hong Kong and southern China III (two volumes). Hong Kong University Press, Hong Kong

Morton B, Tseng CK (eds) (1982) The marine flora and fauna of Hong Kong and southern China (two volumes). Hong Kong University Press, Hong Kong

Motomura H, Matsuura K (eds) (2010) Fishes of Yaku-shima Island—a world heritage island in the Osumi Group, Kagoshima Prefecture, southern Japan. National Museum of Nature and Science, Tokyo

Motomura H, Matsuura K (eds) (2014) Field guide to fishes of Yoron Island in the middle of the Ryukyu Islands, Japan. The Kagoshima University Museum, Kagoshima and the National Museum of Nature and Science, Tsukuba [in Japanese]

Motomura H, Dewa S, Furuta K, Matsuura K (eds) (2013) Fishes of Iou-jima and Take-shima islands, Mishima, Kagoshima, Japan. The Kagoshima University Museum, Kagoshima and the National Museum of Nature and Science, Tsukuba [in Japanese]

Murakami C, Adrianov AV, Shirayama Y (2001) Taxonomic study of the Kinorhyncha in Japan. 1. *Pycnophyes tubuliferus* Adrianov, 1989 (Kinorhyncha: Homalorhagida) from Japan. Publ Seto Mar Biol Lab 39:113–127

Nagasawa K, Uyeno D (2014) A checklist of copepods of the family Pennellidae (Siphonostomatoida) from fishes and whales in Japanese waters (1916–2014). Biosphere Sci 53:43–71 [in Japanese with English abstract]

Nagasawa K, Yamauchi T, Umino T (2008) Synopsis of leeches of the families Piscicolidae and Ozobranchidae (Annelida, Rhynchobdellida) in Japan (1895–2008). Bull Biogeogr Soc Jpn 63: 151–171 [in Japanese with English abstract]

Nagasawa K, Uyeno D, Ho J-S (2013) A checklist of copepods of the family Chondracanthidae (Poecilostomatoida) from fishes in Japanese waters (1918–2013). Biosphere Sci 52:117–143 [in Japanese with English abstract]

Nakabo T (ed) (2013) Fishes of Japan with pictorial keys to the species, 3rd edn. Tokai University Press, Hadano [in Japanese]

Nakamura T (1666) Ryū-gyo [dragons and fish], chū-kai [insects and others]. Kinmouzui, vol. 11. Yamagataya. Available at http://dl.ndl.go.jp/info:ndljp/pid/2569350

Nakamura K, Hikida T, Matsui M (1988) Systematic zoology, vol 9–5: Reptilia (1). Nakayama-Shoten, Tokyo [in Japanese]

Nakano H, Kakui K, Kajihara H, Shimomura M, Jimi N, Tomioka S, Tanaka H, Yamasaki H, Tanaka M, Izumi T, Okanishi M, Yamada Y, Shinagawa H, Sato T, Tsuchiya Y, Omori A, Sekifuji M, Kohtsuka H (2015) JAMBIO coastal organism joint surveys reveals undiscovered biodiversity around Sagami Bay. Region Stud Mar Sci (in press)

Naruse T, Chan T-Y, Tan HH, Ahyong ST, Reimer JD (eds) (2012) Scientific results of the Kumejima marine biodiversity expedition—KUMEJIMA 2009. Zootaxa 3367:1–280

National Science Museum (ed) (1997) Deep-sea fauna and pollutants in Suruga Bay, National museum of nature and science monographs 12. National Museum of Nature and Science, Tokyo

National Science Museum (ed) (2006a) Study on environmental changes in the Sagami Sea and adjacent coastal area with time serial comparison of fauna and flora. I. Marine organisms (brown algae and animals (sponges–annelids)). Mem Natl Sci Mus Tokyo 40:1–408

National Science Museum (ed) (2006b) Study on environmental changes in the Sagami Sea and adjacent coastal area with time serial comparison of fauna and flora. II. Marine organisms (animal (arthropod–chordates)). Mem Natl Sci Mus Tokyo 41:1–575

National Science Museum (ed) (2006c) Study on environmental changes in the Sagami Sea and adjacent coastal area with time serial comparison of fauna and flora. III. Living organisms and soil of coastal areas. Mem Natl Sci Mus Tokyo 42:1–310

National Science Museum (ed) (2007) Fauna Sagamiana. Tokai University Press, Hadano [in Japanese]

Nishikawa T (1980) Ascidians from the coast of Kii Peninsula, Middle Japan, with descriptions of two new species. Mem Natl Sci Mus Tokyo 13:97–111

Nishikawa T (1982) Some ascidians collected in the vicinity of Shimoda, Izu Peninsula, Middle Japan. Mem Natl Sci Mus Tokyo 15:203–212

Nishikawa T (1984) Ascidians collected in the vicinity of the Oga Peninsula, the Japan Sea. Mem Natl Sci Mus Tokyo 17:149–161

Nishikawa T (1986) Some ascidians dredged around the Oki Islands, the Japan Sea. Mem Natl Sci Mus Tokyo 19:175–184

Nishikawa T (2004) A new deep-water lancelet (Cephalochordata) from off Cape Nomamisaki, SW Japan, with a proposal of the revised system recovering the genus *Asymmetron*. Zool Sci 21:1131–1136

Nishimura S (1992a) Guide to seashore animals of Japan with color pictures and keys, vol I. Hoikusha, Osaka [in Japanese]

Nishimura S (1992b) Charenjāgou tanken [The *Challenger* expedition]. Chūōkōronsha, Tokyo [in Japanese]

Nishimura S (1995) Guide to seashore animals of Japan with color pictures and keys, vol II. Hoikusha, Osaka [in Japanese]

Nunomura N (1985) Marine isopod crustaceans in the coast of Toyama Bay. Mem Natl Sci Mus Tokyo 18:121–139

O'Dor R (2004) A census of marine life. BioScience 54:92–93

Ohtsuka S, Boxshall GA (2004) A new species of the deep-sea copepod genus *Scutogerulus* (Calanoida: Arietellidae) from the hyperbenthic waters of Okinawa, Japan. Syst Biodivers 2: 49–55

Ohtsuka S, Boxshall GA, Fosshagen A (2003) A new species of *Neoscolecithrix* (Crustacea; Copepoda; Calanoida) from off Okinawa, southwestern Japan, with comments on the generic position in the superfamily Clausocalanoidea. Bull Natl Sci Mus Tokyo Ser A 29:53–63

Ohtsuka S, Shimomura M, Kitazawa K (2012) A new species of *Enterognathus* (Copepoda, Cyclopoida, Enterognathidae) collected from the Seto Inland Sea, western Japan. ZooKeys 180:1–8

Oka A (1890) Soushū Miura Misaki nite etaru naikou porizoa [On Polyzoa Entoprocta collected in Misaki (Sagami: Miura)]. Zool Mag 2:233–237

Okanishi M, Fujita T (2011) A taxonomic review of the genus *Astrocharis* Koehler (Echinodermata: Ophiuroidea: Asteroschematidae), with a description of a new species. Zool Sci 28:148–157

Okutani T (ed) (2000) Marine mollusks in Japan. Tokai University Press, Hadano

Okutani T (2015) Cuttlefishes and squids of the world, new edition. Tokai University Press, Hadano

Okutani T, Matsukuma A (1982) Some interesting mollusks dredged from the shelf around the southern coast of the Izu Peninsula, Honshu, with descriptions of two new species. Mem Natl Sci Mus Tokyo 15:163–180, pls 9–10

Okutani T, Uchida T, Iwata F (1999) Systematic zoology, vol. 5: Mollusca. Nakayama-Shoten, Tokyo [in Japanese]

Okutani T, Fujikura K, Sasaki T (2004) Two new species of *Bathymodiolus* (Bivalvia: Mytilidae) from methane seeps on the Kuroshima Knoll off the Yaeyama Islands, southwestern Japan. Venus 62:97–110

Reuscher MG, Fiege D, Imajima M (2015) Ampharetidae (Annelida: Polychaeta) from Japan. Part III: The genus *Amphicteis* Grube, 1850 and closely related genera. J Mar Biol Assoc UK 95(5):929–940

Sato T (1936) Vorläufige Mitteilung über *Atubaria heterolopha* gen. nov. sp. nor., einen in freiem Zustand aufgefundenen Pterobranchier aus dem Stillen Ozean. Zool Anz 115:97–106

Shiino S (1964) Systematic zoology, vol 7–1: Crustacea. Nakayama-Shoten, Tokyo [in Japanse]

Shimada D, Kajihara H (2014) Two new species of free-living marine nematodes of *Adoncholaimus* Filipjev, 1918 (Oncholaimida: Oncholaimidae: Adoncholaiminae) from Hokkaido, northern Japan, with a key to species and discussion of the genus. Nematology 16:437–451

Shimada D, Kajihara H, Mawatari SF (2009) Three new species of free-living marine nematodes (Nematoda: Enoplida) from northern Japan. Species Divers 14:137–150

Shimada D, Kakui K, Kajihara K (2012) A new species of deep-sea nematode, *Micoletzkyia mawatarii* sp. nov. (Nematoda: Enoplida: Phanodermatidae) from northern Japan. Species Divers 17:221–226

Shimomura M (2005) *Microjaera morii* sp. nov., a new interstitial isopod from Japan (Crustacea: Janiridae). Bull Kitakyushu Mus Nat Hist Hum Hist Ser A Nat Hist 3:115–120

Shimomura M (2008) *Bathycopea* (Isopoda: Sphaeromatidea: Ancinidae) from Japan, with descriptions of two new species and description of *B. parallela* Birstein. Zootaxa 1678:25–49

Shimomura M (2009) Ten new species of paramunnid isopods (Peracarida: Asellota: Paramunnidae) from Kyushu, southern Japan. Bull Natl Mus Nat Sci Ser A Suppl 3:47–88

Shimomura M, Akiyama T (2008) Description of a new species of Cephalocarida, *Sandersiella kikuchii*, and redescription of *S. acuminata* Shiino based upon the type material. J Crust Biol 28:572–579

Shimomura M, Fujita Y (2009) First record of the thermosbaenacean genus *Halosbaena* from Asia: *H. daitoensis* sp. nov. (Peracarida: Thermosbaenacea: Halosbaenidae) from an anchialine cave of Minamidaito-jima Is., in Okinawa, southern Japan. Zootaxa 1889:55–64

Shimomura M, Kakui K (2012) A new species of *Stegidotea* Poore, 1985 (Isopoda, Chaetiliidae) from Japan. Crustaceana Monogr 17:303–314

Shimomura M, Mawatari SF (2002) A revision of *Heterosignum* (Asellota, Isopoda, Paramunnidae) with descriptions of three new species. J Nat Hist 36:2103–2126

Shimomura M, Ohtsuka S, Tomikawa K (2006) *Ingolfiella inermis* n. sp., a new interstitial ingolfiellid amphipod from Okinawa, southern Japan (Peracarida, Amphipoda). Crustaceana 79:1097–1105

Shimomura M, Fujita Y, Naruse T (2012) First record of the genus *Thetispelecaris* Gutu & Iliffe, 1998 (Crustacea: Peracarida: Bochusacea) from a submarine cave in the Pacific Ocean. In: Naruse T, Chan T-Y, Tan HH, Ahyong ST, Reimer JD (eds) Scientific results of the Kumejima marine biodiversity expedition—KUMEJIMA 2009. Zootaxa 3367:69–78

Shinohara G, Yabe M (2009) A new genus and species of prickleback (Perciformes: Stichaeidae) from Japan. Ichthyol Res 56:394–399

Shinohara G, Endo H, Matsuura K (1996) Deep-water fishes collected from the Pacific coast of northern Honshu, Japan. Mem Natl Sci Mus Tokyo 29:153–185

Smith CR, Kukert H, Wheatcroft RA, Jumars PA, Deming JW (1987) Vent fauna on whale remains. Nature (Lond) 341:27–28

Song S-J, Dahms H-U, Khim J-S (2012) A review of *Leptocaris* including a description of *L. ryukyuensis* sp. nov. (Copepoda: Harpacticoida: Darcythompsoniidae). J Mar Biol Assoc UK 92:1073–1081

Sørensen MV, Herranz M, Rho HS, Min W, Yamasaki H, Sánchez N, Pardos F (2012) On the genus *Dracoderes* Higgins & Shirayama, 1990 (Kinorhyncha: Cyclorhagida) with a redescription of its type species, *D. abei*, and a description of a new species from Spain. Mar Biol Res 8: 210–232

Takahashi Y, Kajihara H, Mawatari SF (2012) A new species of *Hedgpethia* (Arthropoda, Pycnogonida, Colossendeidae) from southwestern Japan. ZooKeys 175:69–74

Takeda M (1977) Crabs of the Ogasawara Islands, V: a collection made by dredging. Mem Natl Sci Mus Tokyo 10:113–140, pls 12–17

Takeda M (1985) Occurrence of a new hermit crab of the genus *Porcellanopagurus* in the Sea of Japan. Mem Natl Sci Mus Tokyo 18:141–144

Takeda M (1993) Four deep-sea species of anomuran crustaceans from Pacific coast of eastern Hokkaido. Mem Natl Sci Mus Tokyo 26:95–100 [in Japanese with English summary]

Takeda M, Kubodera T (1998) A small collection of crabs from the East China Sea. Mem Natl Sci Mus Tokyo 31:211–222

Takeda D, Hashimoto J, Ohta S (2000) New species of the family Bathyograeidae (Crustacea, Decapoda, Brachyura) from the hydrothermal vents along volcanic front of the Philippine Sea Plate. Bull Natl Sci Mus Tokyo Ser A 26:159–172

Tanaka H, Tsukagoshi A (2010) Two new interstitial species of the genus *Parapolycope* (Crustacea: Ostracoda) from central Japan. Zootaxa 2500:39–57

Tanaka H, Tsukagoshi A (2013a) Description and scanning electron microscopic observation of a new species of the genus *Polycopetta* (Crustacea, Ostracoda, Cladocopina) from an interstitial habitat in Japan. ZooKeys 294:75–91

Tanaka H, Tsukagoshi A (2013b) The taxonomic utility of the male upper lip morphology in the ostracod genus *Parapolycope* (Crustacea), with descriptions of two new species. J Nat Hist 47: 963–986

Tanaka H, Tsukagoshi A (2014) Intraspecific variation in male upper lip morphology of *Parapolycope watanabei* n. sp. (Crustacea: Ostracoda) and its implications for speciation. Zool Sci 31:758–765

Tanaka H, Tsukagoshi A, Hiruta S (2010) A new combination in the genus *Parapolycope* (Crustacea: Ostracoda: Myodocopa: Cladocopina), with the description of a new species from Japan. Species Divers 15:93–108

Tanaka H, Tsukagoshi A, Karanovic I (2014) Molecular phylogeny of interstitial Polycopidae ostracods (Crustacea) and descriptions of a new genus and four new species. Zool J Linn Soc 172:282–317

Tokioka T, Uchida T, Tanita S (1961) Systematic zoology, vol 2: Mesozoa, Porifera, Coelenterata, Ctenophora. Nakayama-Shoten, Tokyo [in Japanese]

Uchida H (1979) Cerianthids (Anthozoa, Coelenterata) from Kii Region, Middle Japan. Mem Natl Sci Mus Tokyo 12:185–199

Uchida T, Matsubara K (1963) Systematic zoology, vol 9–1: Pisces (1). Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Yagyu R (1962) Systematic zoology, vol 1: Overview, Protozoa. Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Mawatari S, Tokioka T (1965a) Systematic zoology, vol 8–1: Archicoelomata, Tentaculata, Chaetognatha, Pogonophora. Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Sudzuki M, Ehara S, Tadano M, Inoue I, Yamada M (1965b) Systematic zoology, vol 4: Aschelminthes. Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Yamashita J, Sawada I, Iwata F, Yamada M (1965c) Systematic zoology, vol 3: Bilateria, Platyhelminthes, Nemertinea, Kamptozoa, Sipunculoidea. Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Utinomi H, Ehara S, Sekiguchi K, Morikawa K, Suzuki S, Yaginuma T (1966) Systematic zoology, vol 7–2: Trilobitomorpha, Merostomata, Arachnida. Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Yamada M, Yamaguchi H, Nagao Z, Kato K, Morikawa K (1967) Systematic zoology, vol 6: Articulata, Annelida, Onychophora, Tardigrada, Pentastomida. Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Tokunaga M, Ando H, Sakagami S, Asahina S, Imadaté G (1970) Systematic zoology, vol 7–3: Insecta (1). Nakayama-Shoten, Tokyo [in Japanese]

Uchida T, Yamada M, Kogo I, Hayashi R, Irimura S, Shigei M, Oguro C (1974) Systematic zoology, vol 8–2: Echinodermata. Nakayama-Shoten, Tokyo [in Japanese]

Ueno M, Asahina S, Yamasaki T, Morimoto K, Kawai T, Tsutsumi C, Kaneko K, Ishihara T, Ueshima N (1971) Systematic zoology, vol 7–5: Insecta (2). Nakayama-Shoten, Tokyo [in Japanese]

Utinomi H, Uchida T, Ehara S, Miyoshi Y, Shinohara K (1966) Systematic zoology, vol 7–3: Ppycnogonida, Myriapoda. Nakayama-Shoten, Tokyo [in Japanese]

Uyeno D (2015) Systematic revision of the pennellid genus *Creopelates* Shiino, 1958 (Copepoda: Siphonostomatoida) and the proposal of a new genus. Zootaxa 3904:359–386

WWF-Japan (2009) Ooura Bay, Okinawa Island—thirty-six (36) new species of crustacean confirmed. http://www.wwf.or.jp/activities/upfiles/Ourawan_PR091125_eng.pdf. Accessed 7 Apr 2015

Yamada S, Tanaka H (2011) First report of an interstitial *Semicytherura* (Crustacea: Ostracoda: Cytheruridae: Cytherurinae): a new species from central Japan. Species Divers 16:49–63

Yamada S, Tanaka H (2013) Two interstitial species of the genus *Semicytherura* (Crustacea: Ostracoda) from Japan, with notes on their microhabitats. Zootaxa 3745:435–448

Yamada S, Tsukagoshi A (2010) Two new species of the genus *Semicytherura* (Podocopa: Ostracoda) from Akkeshi Bay, Hokkaido, Japan, with comments on the speciation and related species. Zool Sci 27:292–302

Yamada S, Tsukagoshi A, Ikeya N (2005) Taxonomy, morphology and speciation of the *Semicytherura henryhowei* group (Crustacea: Ostracoda). Hydrobiologia 538:243–265

Yamasaki H, Fujimoto S (2014) Two new species in the *Echinoderes coulli* group (Echinoderidae, Cyclorhagida, Kinorhyncha) from the Ryukyu Islands, Japan. ZooKeys 382:27–52

Yamasaki H, Kajihara H (2012) A new brackish-water species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Seto Inland Sea, Japan. Species Divers 17:109–118

Yamasaki H, Kajihara H, Mawatari SF (2012) First report of kinorhynchs from Hokkaido, Japan, including a new species of *Pycnophyes* (Pycnophyidae: Homalorhagida). Zootaxa 3425:23–41

Yokoyama M (1890) Versteinerungen aus der japanischen Kreide. Palaeontographica 36:159–202

Part II
Terrestrial Animals

Chapter 3
A Review of the Processes of Mammalian Faunal Assembly in Japan: Insights from Molecular Phylogenetics

Jun J. Sato

Abstract To elucidate the origins of the Japanese mammalian fauna from the perspectives of biogeography and community ecology, I reviewed molecular phylogenetic and phylogeographic studies for all non-volant terrestrial mammals indigenous to the Japanese Archipelago (63 species), with a particular focus on obtaining reliable chronological data. The results of this review demonstrate that geological vicariance events in the Tsugaru and Korea (Tsushima) Straits can explain the distribution of many Japanese mammals, in particular the Hokkaido-endemic species with Late Pleistocene origins and the Honshu–Shikoku–Kyushu-endemic species with Middle Pleistocene or earlier origins. Phylogenetic relatedness also contributed to the observed patterns of distribution through the processes of competitive exclusion and species assortment, and abiotic environmental filtering was another important factor. Later colonists of Honshu–Shikoku–Kyushu, from northern Hokkaido or the southern Tsushima Islands, were mostly excluded owing to the competitive dominance of earlier residents or environmental filtering. On the other hand, the fragmented distributions of some species with more ancient origins in both Hokkaido and Honshu–Shikoku–Kyushu may be a result of the competitive dominance of later migrants. Ecological coexistence can be achieved by phylogenetically dispersed species, supporting the principle of species assortment. Because almost all aspects of the mammalian faunal assembly in Japan can be explained by geological events or community ecological processes, the Japanese Archipelago may be an ideal model island system in which to study the mechanisms of faunal assembly.

Keywords Mammals • The Japanese Archipelago • Molecular phylogenetics • Phylogeography • Community ecology • Faunal assembly

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3.1 The Factors That Shape Species Diversity

The construction of floral and faunal assemblages is an important theme of research in ecology, evolution, systematics, conservation biology, and other biological sciences. Biological communities are assembled not at random but rather by various deterministic biotic and abiotic processes (e.g., Sato 2013). For example, in continental island systems such as the Japanese Archipelago, geographic separation has had a dominant influence on the characteristics of faunal assemblages. Based on the distribution and systematics of flora and fauna among Japanese islands, researchers have deduced the influence of past geological events on both extant and extinct species, particularly mammals (Dobson 1994; Dobson and Kawamura 1998; Kawamura 1998; Millien-Parra and Jaeger 1999; McKay 2012). Although much fruitful research has been carried out based on fossil evidence (Kawamura et al. 1989; Kawamura 1991, 1994), the paucity of fossil remains in the Japanese Archipelago is a major obstacle to understanding the origins of Japanese mammals. Recent advances in molecular phylogenetics provide techniques for dating lineage divergence in species with poor paleontological records. However, the time scale for the diversification of Japanese mammals has not been discussed from a synthetic point of view with a focus on molecular chronology for a broad spectrum of taxonomic groups.

Recently, abundant data on molecular phylogenetics and phylogeography have been generated for various mammalian taxa. These data provide an unprecedented opportunity to clarify the chronology of the migration, divergence, and range expansion of Japanese mammals. Although some studies have examined these molecular data, the mammalian species assembly remains incompletely understood. For example, McKay (2012) used molecular data to analyze the assembly process for a relatively large number of mammalian species in Japan. However, the chronological estimates in McKay (2012) were largely incongruent with fossil and geological evidence, which may have resulted from the evolutionary rate being inappropriately calibrated (see Appendix).

Similarly, although ecological and phylogenetic factors have crucial roles in shaping species composition (Webb et al. 2002; Gillespie 2004; Dayan and Simberloff 2005; Emerson and Gillespie 2008), they are not well understood. For example, ecological theory has traditionally suggested that phylogenetically close species are less likely to coexist because they are more likely to have similar niches and therefore experience competitive exclusion. Distantly related species, on the other hand, are more likely to have different niche requirements and thus be able to avoid competition by a process called “species assortment” (Dayan and Simberloff 2005; Emerson and Gillespie 2008). In fact, it has been suggested that mammalian assemblages tend to be composed of species that are distantly related (Cardillo et al. 2008; Cooper et al. 2008), implying that competitive interactions are important in the formation of mammal communities. Character displacement could be another mechanism for the coexistence of closely related species (Dayan and Simberloff

2005). Thus, there are clearly a number of ecological and phylogenetic factors for the establishment of biota.

Sato (2013) reviewed molecular phylogenetic and feeding ecological studies for species in the family Mustelidae (Mammalia, Carnivora), and concluded that geological, ecological, and phylogenetic factors have had an uneven and species-dependent influence on the formation of the mustelid fauna in the Japanese Archipelago. This type of approach provides important insights into the underlying mechanisms for island species assembly and helps us to develop a comprehensive understanding of the diversity and endemism of island organisms, which is in line with recent trends in conservation biology (Frankham et al. 2010). In this chapter, I review molecular phylogenetic and phylogeographic research on non-volant terrestrial mammals in Japan to help elucidate the processes that have produced and maintained Japanese mammalian species diversity. Islands have been considered ideal model systems for ecology, evolution, biogeography, and conservation biology (Kueffer et al. 2014; Warren et al. 2015). I attempt to construct here a general theory of island biology by summarizing empirical case studies for each mammalian species in Japan.

3.2 Mammals in the Japanese Archipelago

The Japanese Archipelago can be divided into three major biogeographic areas based on faunal differences: Hokkaido, Honshu–Shikoku–Kyushu (hereafter designated as HSK), and the Ryukyu Islands (Fig. 3.1) (Kawamura 1991, 1994, 1998; Dobson 1994; Dobson and Kawamura 1998). These major islands are thought to have been connected to the Asian continent through land bridges formed in past geological periods (e.g., during glacial periods in the Pleistocene), which allowed many migrant species from the Asian continent to reach the islands before becoming isolated in each region (Dobson 1994; Millien-Parra and Jaeger 1999). The oldest lineage of Japanese mammals is believed to have persisted since the origin of the Japanese islands in the Miocene or earlier [about 15 MYA (million years ago)] (Neall and Trewich 2008). Each lineage has its own particular origin, and various levels of endemism are observed among the major islands (Suzuki 2015). For example, most terrestrial mammals in Hokkaido are also found on the continent, whereas species in HSK and especially in the Ryukyus are highly endemic, and generally are not found on the continent (Suzuki 2015). In short, it is clear that differences in the patterns of past land bridges have affected the mammalian faunal constitution of the Japanese Archipelago.

There are 63 mammalian species in the Japanese Archipelago, excluding marine-adapted, volant, and artificially introduced species (Ohdachi et al. 2015). These species are classified into 15 families spanning 6 orders within the Boreoeutheria (Euarchontaglires and Laurasiatheria): Eulipotyphla (Soricidae, 12; Talpidae, 8), Primates (Cercopithecidae, 1), Rodentia (Gliridae, 1; Sciuridae, 6; Muridae, 10; Cricetidae, 6), Lagomorpha (Leporidae, 3; Ochotonidae, 1), Carnivora

Fig. 3.1 A schematic configuration of the islands around the Japanese Archipelago [Sakhalin, Hokkaido, Etorofu, Kunashiri, Honshu, Sado, Shikoku, Kyushu, Tsushima, Ryukyu (Amami-Oshima, Tokunoshima, and Okinawajima), Iriomotejima, Jeju, the Taiwan Islands] and major straits [Tatar (Mamiya), La Perouse (Soya), Tsugaru, Korea (Tsushima), Tokara, and Kerama). The Echigo Plain is depicted on Honshu Island. Honshu, Shikoku, and Kyushu Islands are combined into *HSK*, as they are in the text

(Felidae, 1; Canidae, 2; Ursidae, 2; Mustelidae, 7), and Cetartiodactyla (Cervidae, 1; Suidae, 1; Bovidae, 1). In this chapter, I first describe the biogeographic patterns for mammals in Japan. I also review molecular phylogenetic and phylogeographic research for each mammalian species, with a particular focus on obtaining reliable chronological data regarding their origins in the Japanese Archipelago. Second, I evaluate the consistency between the estimated time scales and past geological events. Finally, I discuss the mechanisms and processes underlying the establishment of the Japanese mammalian fauna in light of community ecology. The biogeographic patterns and dates of divergence between Japanese mammals and their closest relatives are summarized in Tables 3.1 and 3.2, and Fig. 3.2.

3.3 Biogeographic Patterns

I aimed to characterize the distributions of the 63 Japanese terrestrial mammal species by ten biogeographic patterns (BP) according to their current distributions, as summarized in Table 3.1 [I considered the fossil species distribution only if available and relevant to the discussion of the faunal assembly (e.g., *Ursus arctos*)]. This process of categorization may overlook some important evolutionary factors; however, considering each distribution separately would not provide meaningful insight into universal processes for faunal assembly. I believe that ten BPs provide an optimal framework for discussing the geological, phylogenetic, and ecological factors pertaining to the mammalian faunal assembly in Japan.

One important assumption made in categorizing these BPs is that species with similar biogeographic patterns are more likely to share a similar phylogenetic history on the geological time scale. The similarity in the phylogenetic history supports nonrandom mechanisms for species assembly. Therefore, in this review, I tested the validity of this assumption.

3.4 Origins and Community Assembly Processes of Japanese Mammals

In this section, I review the results of molecular phylogenetic and phylogeographic research on Japanese mammals (readers are recommended to refer to the Appendix for further details). In some cases, it was not possible to find chronological information based on molecular data for the species (or lineages) or the most closely related continental species (or lineages) within the existing literature (e.g., *Suncus murinus*, *Mogera uchidai*, *Apodemus agrarius*). In other cases, I did not include a species in the discussion because of the likelihood of human introduction (e.g., *Mus caroli*). In obtaining chronological data from published research, I tried to include data from studies in which nuclear genes, rather than mitochondrial genes, were used to examine phylogenetic relationships among distantly related species; owing to the genetic saturation phenomenon, rapidly evolving mitochondrial genes are notoriously unreliable for inferring phylogenies and divergence times, particularly at deeper nodes (e.g., >6 MYA for the Murinae rodents; Steppan et al. 2005). Conversely, I used time estimates based largely on mitochondrial DNA data when examining relationships among closely related species and intraspecific

Table 3.1 Descriptions of the biogeographic patterns

Categories	Descriptions	Species
BP1	Present only in Hokkaido in Japan with the same species expanded to the continental Holarctic region	Northern red-backed vole, *Myodes rutilus*
BP2	Present only in Hokkaido in Japan with the same species also occurring in the continental Palaearctic region	Eurasian least shrew, *Sorex minutissimus*
		Eurasian common shrew, *Sorex caecutiens*
		Long-clawed shrew, *Sorex unguiculatus*
		Slender shrew, *Sorex gracillimus*
		Eurasian red squirrel, *Sciurus vulgaris*
		Siberian chipmunk, *Tamias sibiricus*
		Siberian flying squirrel, *Pteromys volans*
		East Asian field mouse, *Apodemus peninsulae*
		Gray red-backed vole, *Myodes rufocanus*
		Northern pika, *Ochotona hyperborea*
		Mountain hare, *Lepus timidus*
		Sable, *Martes zibellina*
BP3	Present in Hokkaido and Sakhalin	Dark red-backed vole, *Myodes rex*
BP4	Present in Hokkaido and a part or all of the Honshu, Shikoku, and Kyushu islands in Japan with the same species also occurring in the Palaearctic, Holarctic, and Oriental region	Red fox, *Vulpes vulpes*
		Raccoon dog, *Nyctereutes procyonoides*
		Brown bear, *Ursus arctos*[a]
		Ermine or stoat, *Mustela erminea*
		Least weasel, *Mustela nivalis*
		Sika deer, *Cervus nippon*
BP5	Endemic to Japan and present in Hokkaido, Honshu, Shikoku, and Kyushu	Large Japanese field mouse, *Apodemus speciosus*
		Small Japanese field mouse, *Apodemus argenteus*
BP6	Endemic to Japan and present in Honshu, Shikoku, and Kyushu	Azumi shrew, *Sorex hosonoi*
		Shinto shrew, *Sorex shinto*
		Japanese water shrew, *Chimarrogale platycephalus*
		Japanese white-toothed shrew, *Crocidura dsinezumi*

(continued)

Table 3.1 (continued)

Categories	Descriptions	Species
		Lesser Japanese shrew mole, *Dymecodon pilirostris*
		Greater Japanese shrew mole, *Urotrichus talpoides*
		Japanese mountain mole, *Euroscaptor mizura*
		Lesser Japanese mole, *Mogera imaizumii*
		Echigo mole, *Mogera etigo*[b]
		Japanese macaque, *Macaca fuscata*
		Japanese dormouse, *Glirulus japonicus*,
		Japanese squirrel *Sciurus lis*
		Japanese giant flying squirrel, *Petaurista leucogenys*
		Japanese flying squirrel, *Pteromys momonga*
		Anderson's red-backed vole, *Myodes* (*Eothenomys*) *andersoni*
		Smith's red-backed vole, *Myodes* (*Eothenomys*) *smithii*
		Japanese field vole, *Microtus montebelli*
		Japanese hare, *Lepus brachyurus*
		Japanese weasel, *Mustela itatsi*
		Japanese marten, *Martes melampus*
		Japanese badger, *Meles anakuma*
		Japanese serow, *Capricornis crispus*
BP7	Present in the Honshu-Shikoku-Kyushu region with the same species also occurring in the continental Palaearctic, Oriental, and Southwest Asian region	Large Japanese mole, *Mogera wogura*
		Harvest mouse, *Micromys minutus*
		Asian black bear, *Ursus thibetanus*
BP8	Present in Honshu, Shikoku, Kyushu, and Ryukyu with the same species also occurring Palaearctic and Oriental regions	Wild boar, *Sus scrofa*

(continued)

Table 3.1 (continued)

Categories	Descriptions	Species
BP9	Present only in the Ryukyu region and adjacent islands	Watase's shrew, *Crocidura watasei*
		Orii's shrew, *Crocidura orii*
		Senkaku mole, *Mogera uchidai*
		Amami spiny rat, *Tokudaia osimensis*
		Okinawa spiny rat, *Tokudaia muenninki*
		Tokunoshima spiny rat, *Tokudaia tokunoshimensis*
		Ryukyu long-furred rat, *Diplothrix legata*
		Amami rabbit, *Pentalagus furnessi*
BP10	Present in southern small islands adjacent to the Japanese main islands with the same species also occurring in the continental Palaearctic and/or Oriental region	Asian lesser white-toothed shrew, *Crocidura shantungensis*
		Musk shrew, *Suncus murinus*
		Striped field mouse, *Apodemus agrarius*
		Ryukyu mouse, *Mus caroli*
		Leopard cat, *Prionailurus bengalensis*
		Siberian weasel, *Mustela sibirica*

[a] Currently confined to Hokkaido but fossil evidence was found in Honshu in the Pleistocene (Kawamura 1994)

[b] Should be the same species as the Sado mole *Mogera tokudae* because the genetic difference between them is at an intraspecific level; see Appendix)

lineages, because genetic saturation is less prevalent at these lower levels of divergence.

Furthermore, I paid much attention to differences in evolutionary rates between inter- and intraspecific variants (time-dependent evolutionary rates) (Ho et al. 2005; Davison et al. 2011) and between different mammalian lineages (lineage-dependent evolutionary rates) (Gissi et al. 2000; Nabholz et al. 2008). I estimated the most plausible time scales, taking into account the differences between these evolutionary rates. Where no molecular chronological data were obtained from previous studies and DNA sequences were available in the DNA database, I calculated the time scales based on the currently most reliable evolutionary rate, with careful consideration of the aforementioned evolutionary rate differences (see Appendix). Recently, the supertree method has become a popular method for assigning temporal structure to phylogenies containing a complete set of species of a certain taxon (e.g., Bininda-Emonds et al. 1999 for Carnivora). However, I did not consider

Table 3.2 Chronological data and their references

BP[a]	Species	Divergence time (MYA)[b]	MRCA (MYA)[f]	References
BP1	*Myodes rutilus*	<0.1	N.A.	Kohli et al. (2015)
BP2	*Sorex minutissimus*	0.07	N.A.	This study (Appendix)
	Sorex caecutiens	0.56	0.09	This study (Appendix)
	Sorex unguiculatus	0.15	0.15	This study (Appendix)
	Sorex gracillimus	0.07	0.05	This study (Appendix)
	Sciurus vulgaris	0.18–0.36	N.A.	This study (Appendix)
	Tamias sibiricus	0.10–0.19	N.A.	This study (Appendix)
	Pteromys volans	0.2–0.4	N.A.	Oshida et al. (2005)
	Myodes rufocanus	0.27	<0.13	Abramson et al. (2012), This study (Appendix)
	Apodemus peninsulae	0.1	N.A.	Sakka et al. (2010)
	Ochotona hyperborea	1.62	N.A.	This study (Appendix)
	Lepus timidus	0.30–0.37	0.17	Kinoshita et al. (2012), This study (Appendix)
	Martes zibellina	0.09	0.04	Kinoshita et al. (2015)
BP3	*Myodes rex*	0.81	0.24–1.16	Abramson et al. (2012), This study (Appendix)
BP4	*Vulpes vulpes*	0.5–2.88[c]	N.A.	This study (Appendix)
	Nyctereutes procyonoides	<0.64	<0.38	This study (Appendix)
	Ursus arctos	0.053–0.194[c]	N.A.	Hirata et al. (2013)
	Mustela erminea	0.13–0.39[c]	N.A.	This study (Appendix)
	Mustela nivalis	0.45–1.02[c]	N.A.	This study (Appendix)
	Cervus nippon	0.3[c]	N.A.	Nagata et al. (1999)
BP5	*Apodemus speciosus*	5.9	0.51	Suzuki et al. (2004, 2008)
	Apodemus argenteus	7.3	0.64	Suzuki et al. (2004, 2008)
BP6	*Sorex hosonoi*	0.75	N.A.	This study (Appendix)
	Sorex shinto	0.8	N.A.	This study (Appendix)
	Chimagogale platycephalus	0.83–0.95	0.27–0.39	Iwasa and Abe (2006), This study (Appendix)
	Crocidura dsinezumi	1.42	0.34	Dubey et al. (2008), this study (Appendix)
	Dymecodon pilirostris	1.9–2.85	1.77–2.65	This study (Appendix)
	Urotrichus talpoides	1.9–2.85	1.15–1.73	This study (Appendix)

(continued)

Table 3.2 (continued)

BP[a]	Species	Divergence time (MYA)[b]	MRCA (MYA)[f]	References
	Euroscaptor mizura	5.21	1.17–1.75	Kirihara et al. (2013)
	Mogera imaizumii	2.31	N.A.	Kirihara et al. (2013)
	Mogera etigo, *M. tokudae*	3.64[d]	N.A.	Kirihara et al. (2013)
	Macaca fuscata	0.38–0.42	N.A.	Chu et al. (2007)
	Glirulus japonicus	24–30	3.0–5.0	Nunome et al. (2007), and Yasuda et al. (2007, 2012)
	Sciurus lis	0.49–1.36	N.A.	This study (Appendix)
	Petaurista leucogenys	1.39–3.06	0.09–0.24	Oshida et al. (2009a, b), this study (Appendix)
	Pteromys momonga	1.2–2.5	N.A.	This study (Appendix)
	Myodes andersoni, *M. smithii*	0.9–2.3[e]	0.77[g]	Luo et al. (2004), Lebedev et al. (2007), Kohli et al. (2014)
	Microtus montebelli	0.95	N.A.	Bannikova et al. (2010)
	Lepus brachyurus	2.48–3.10	1.07–1.2	Nunome et al. (2010, 2014), this study (Appendix)
	Mustela itatsi	1.5–1.6	0.83–1.17	Masuda et al. (2012), Sato et al. (2012)
	Martes melampus	1.0–1.1	N.A.	Li et al. (2013)
	Meles anakuma	0.5	0.11–0.23	Tashima et al. (2011)
	Capricornis crispus	0.85–1.0	0.09	Okumura (2004), Liu et al. (2013), This study (Appendix)
BP7	*Mogera wogura*	1.2	N.A.	Kirihara et al. (2013)
	Micromys minutus	<0.08	N.A.	Yasuda et al. (2005)
	Ursus thibetanus	0.96–1.71	N.A.	This study (Appendix)
BP8	*Sus scrofa leucomystax*	0.29	N.A.	This study (Appendix)
	Sus scrofa riukiuanus	<0.66	N.A.	This study (Appendix)
BP9	*Crocidura watasei*	1.11	N.A.	Dubey et al. (2008)
	Crocidura orii	5.42	N.A.	Dubey et al. (2008)
	Mogera uchidai	N.A.	N.A.	N.A.
	Tokudaia	6.5–8.1	2.58	Sato and Suzuki (2004), This study (Appendix)
	Diplothrix legata	2.11–3.17	N.A.	This study (Appendix)
	Pentalagus furnessi	8.63	N.A.	Matthee et al. (2004)

(continued)

Table 3.2 (continued)

BP[a]	Species	Divergence time (MYA)[b]	MRCA (MYA)[f]	References
BP10	*Crocidura shantungensis*	0.1	N.A.	This study (Appendix)
	Suncus murinus	N.A.	N.A.	N.A.
	Apodemus agrarius	N.A.	N.A.	N.A.
	Mus caroli	N.A.	N.A.	N.A.
	Mustela sibirica	0.56–0.8	N.A.	This study (Appendix)
	Prionailurus bengalensis euptilurus	0.07	N.A.	This study (Appendix)
	Prionailurus bengalensis iriomotensis	0.26	N.A.	This study (Appendix)

[a] Biogeographic pattern (BP) (see text)

[b] Divergence time of the species (lineage) in Japan (MYA, million years ago) from the most closely related continental or the other major Japanese Island species (lineage)

[c] Multiple migrations were suggested around or during these times (see Appendix for each time for the multiple migrations)

[d] Divergence time of the clade including *Mogera etigo* and *Mogera tokudae* from the most closely related lineage. This treatment was because they should be considered the same species

[e] Divergence time of the clade including *Myodes andersoni* and *Myodes smithii* from the most closely related lineage. This treatment was because they should be considered the same species

[f] Most Recent Common Ancestor of the lineages present in Japan (MYA, million years ago)

[g] Divergence time of the most divergent Shikoku lineage in the *M. andersoni*-*M. smithii* complex

time estimates from the supertree method, because such estimates are often inconsistent with the fossil record and other supermatrix estimates (Sato and Wolsan 2016).

After reviewing the molecular phylogenetic and phylogeographic studies, I summarized in Table 3.2 and Fig. 3.2 the divergence times of each Japanese mammal from closely related continental species (or lineages) and, where possible, the date of divergence from the most recent common ancestor (MRCA) of each Japanese mammal. Here, I assumed that the divergence time from closely related continental species (lineages) indicates the origin of each Japanese mammal. Furthermore, it should be noted that I implicitly assumed that extant Japanese mammals were derived from continental species, and did not consider the converse, that is, that the Japanese Archipelago may have been a “source” for the continental species or lineages.

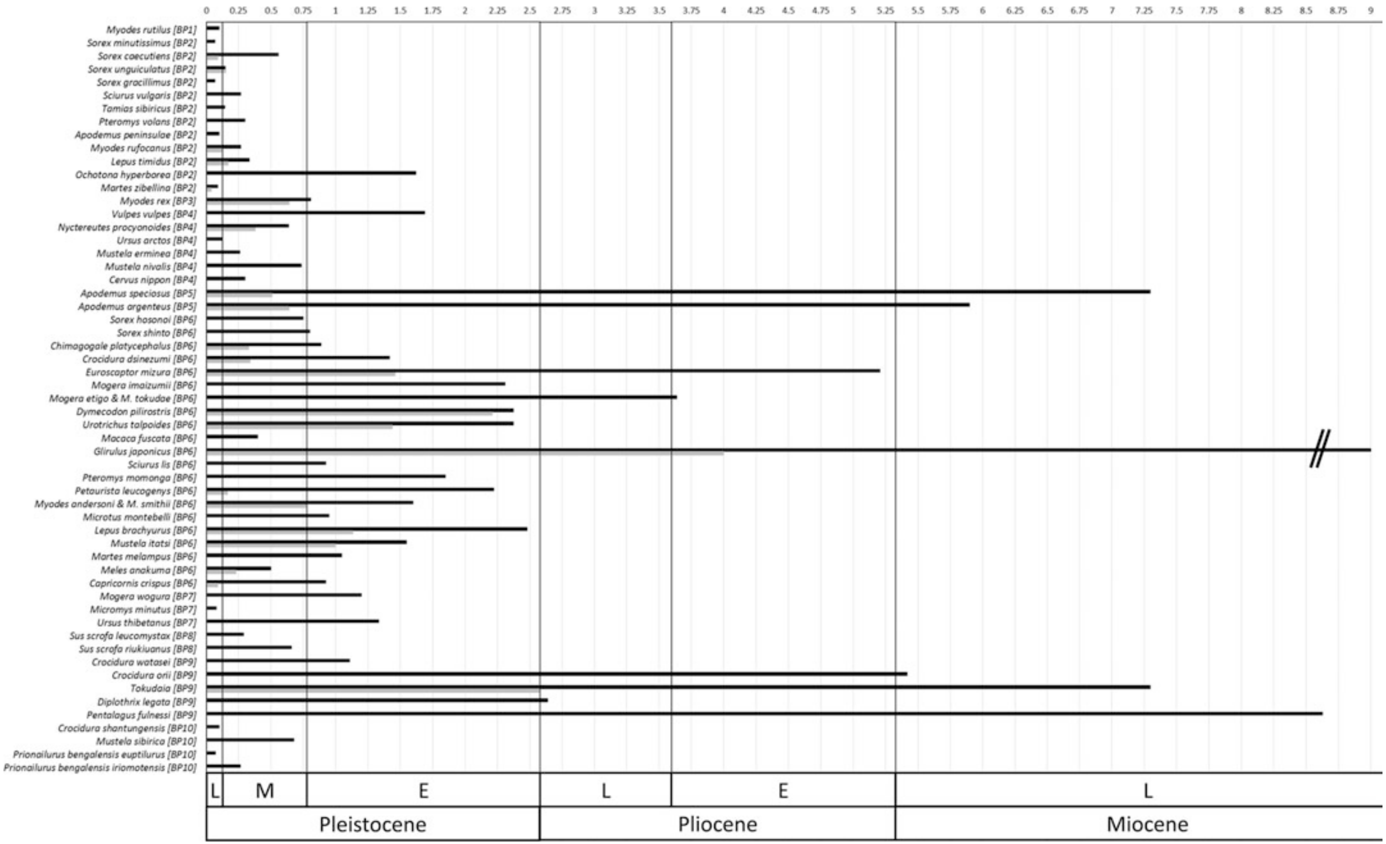

Fig. 3.2 Dates of divergence (*black horizontal bar*) and dates of the most recent common ancestor (MRCA; *gray horizontal bar*) of Japanese mammals (species or intraspecific lineages), averaged between the maximum and minimum values listed in Table 3.2. Species names and biogeographic patterns are listed on the *y*-axis. The units for the upper *x*-axis are millions of years (MYA). L, M, and E above the name of each geological period mean Late, Middle, and Early, respectively. The *horizontal bar* for *Glirulus japonicus* is cut because its date of divergence (27 MYA) is quite old compared with the other mammals in Japan

3.4.1 Geological Explanations for the Mammalian Species Assembly in Japan

In general, species found in Hokkaido (with BP1, BP2, and BP3) appear to have the most recent origins among Japanese mammals, with most of the species (12 of 14) originating in the late Middle to Late Pleistocene. The 2 remaining species (*Ochotona hyperborea* and *Myodes rex*) have more ancient Early Pleistocene origins (Fig. 3.2). Similarly, HSK, the other major island region in Japan, also contains species (with BP6) with more ancient origins than the Hokkaido-endemic species. Most HSK species with BP6 have Early Pleistocene or older origins, except for 3 of 26 species (*Sorex hosonoi*, *Macaca fuscata*, and *Meles anakuma*), which have more recent Middle Pleistocene origins (Fig. 3.2). This observation is consistent with reports in the existing literature that there are older and more differentiated species in the HSK region than in northernmost Hokkaido (e.g., Millien-Parra and Jaeger 1999), suggesting that the effects of past geological vicariance events by the Tsugaru and Korea (Tsushima) Straits may have contributed to the higher extent of endemism among the mammalian species in the HSK region. The highly endemic trend of the Ryukyu mammals (with BP9; Fig. 3.2) is also concordant with the features of the Ryukyu Islands, which are isolated by deep water, including the Tokara and Kerama Straits (Kimura 2000) (Fig. 3.1).

In total, 5 of 14 species with BP1, BP2, and BP3 endemic to Hokkaido in Japan (*Myodes rutilus*, *Sorex minutissimus*, *Sorex gracillimus*, *Apodemus peninsulae*, *Martes zibellina*) have Late Pleistocene origins (Fig. 3.2). Their biogeographic pattern (present in Hokkaido and absent in more southern islands) and their Late Pleistocene origins are congruent with the idea that the Tsugaru Strait, established in the Late Pleistocene, would have prevented dispersal from Hokkaido to Honshu and more southern major islands (Ohshima 1991). It should be noted that, although the resulting distribution patterns in Japan are similar, the dispersal events in the continent leading to the migrations into Hokkaido would have differed among BP1, BP2, and BP3 species. For instance, the source of the population expansions of *A. peninsulae* and *M. zibellina* (BP2) was most likely the Russian Far East, where genetic diversity is estimated to be higher, suggesting the existence of refugia during glacial periods (Serizawa et al. 2002; Sakka et al. 2010; Kinoshita et al. 2015). Meanwhile, *Myodes rutilus* (BP1) is more likely to derive from a northern refugium called Beringia (Kohli et al. 2015). Different evolutionary histories are also inferred among the 4 *Sorex* species in Hokkaido (*S. minutissimus*, *S. caecutiens*, *S. unguiculatus*, and *S. gracillimus*), even within the same biogeographic pattern (BP2) (Ohdachi et al. 2001; also see Appendix). Among these species, different evolutionary processes appear to have generated similar distribution patterns.

The other 9 of 14 species endemic to Hokkaido (*Sorex caecutiens*, *Sorex unguiculatus*, *Sciurus vulgaris*, *Tamias sibiricus*, *Pteromys volans*, *Myodes rufocanus*, *Lepus timidus*, *Ochotona hyperborea*, and *Myodes rex*) have more ancient origins in the Middle Pleistocene or earlier. *Ochotona hyperborea* and *Myodes rex*, whose distributions are currently restricted to alpine areas and fragmented forests, respectively, in Hokkaido, appear to have the most ancient origins, in the Early Pleistocene (Fig. 3.2). It is not clear why species originating in the Middle Pleistocene or earlier did not migrate into Honshu, given the presence of land bridges between Hokkaido and Honshu during this period. One explanation may be that their demographic expansion occurred more recently. In fact, the lineage divergences of *S. caecutiens* and *M. rufocanus* in Hokkaido are inferred to have occurred in the Late Pleistocene (see Appendix). Thus, the Tsugaru Strait would have been a geographical barrier for species that originated in the Middle Pleistocene and underwent Late Pleistocene expansions. Alternatively, this phenomenon may be explained by biotic competitive recessiveness or abiotic environmental filtering (Kraft et al. 2015) in Honshu and the more southern islands (see Sect. 3.4.2).

On the other hand, all the BP6 species endemic to the HSK region have origins before the onset of the Late Pleistocene (Table 3.2 and Fig. 3.2), suggesting that no migration occurred from Hokkaido in the Late Pleistocene. It should be noted, however, that fossil evidence suggests that some extinct large herbivores (the Eurasian elk *Alces alces*, the auroch *Bos primigenius*, and the steppe bison *Bison priscus*) migrated into HSK from Hokkaido via ice bridges temporarily formed in the Tsugaru Strait in the Late Pleistocene (Kawamura 1991, 1994). The older origins of BP6 species are also consistent with geological evidence suggesting that the Tsugaru and Korea (Tsushima) Straits functioned as barriers against inter-island mammal dispersal in the Late Pleistocene period (Ohshima 1991).

It is not clear whether the BP6 species migrated via the northern Tsugaru Strait or the southern Korea (Tsushima) Strait. However, we can make inferences based on the distributions of the most closely related species. Because BP6 species are absent from Hokkaido, it is parsimonious to assume that they migrated into the HSK region through the southern Korea (Tsushima) Strait. This southern route migration hypothesis is also supported by the presence of closely related species on the Korean Peninsula and in other southern continental regions. Conversely, if the BP6 species migrated via the northern route, we would have to assume that they later became extinct in Hokkaido. Therefore, it is reasonable to suppose that *Chimarrogale platycephalus*, *Euroscaptor mizura*, *Macaca fuscata*, *Petaurista leucogenys*, and *Capricornis crispus*, whose closest relatives are distributed in the southern part of the Eurasian continent (South China, Southeast Asia, and Taiwan), migrated via the southern route.

Nevertheless, it is possible that some Japanese species might have arrived via the northern route. For example, the closest relatives of *Martes melampus* in the subgenus *Martes* are all observed in the northern Eurasian and American continent and do not exist in the Korean Peninsula. Thus, *M. melampus* has been suggested to have migrated into the Japanese Archipelago via Hokkaido (Ishida et al. 2013).

Although the reason for the current absence of *M. melampus* in Hokkaido (except for descendants of the introduced individuals) is not clear, Ishida et al. (2013) implied the existence of interspecific hybridization between *M. zibellina* and a species closely related to *M. melampus* and *M. americana*, suggesting that the earlier resident *M. melampus* became extinct by assimilation or competitive interaction with the later colonist *M. zibellina*.

The closest relative to the *Myodes andersoni–Myodes smithii* complex in the HSK region is the clade consisting of *Myodes rufocanus* and *Myodes rex*, both of which inhabit Hokkaido and are not present in the Korean Peninsula, which supports the northern route migration hypothesis for the *M. andersoni–M. smithii* complex. Again, it is uncertain how the ancestral lineage of the *M. andersoni–M. smithii* complex disappeared from Hokkaido. However, the fact that *Myodes rex* (the oldest *Myodes* lineage in Hokkaido) shows fragmented distribution may indicate that the older residents went extinct by competitive interactions after new arrivals of congeneric relatives in different ages (see Sect. 3.4.2). It may be that the ancestral lineage of the *M. andersoni–M. smithii* complex was excluded in Hokkaido by competitive interactions with the new migrants (*M. rex* and *M. rufocanus*; see Sect. 3.4.2).

However, no traces of the BP6 species derived from the southern route in the Middle Pleistocene or earlier are found in Hokkaido, despite the presence of land bridges during this time. This observation implies that BP6 species did not cross the Tsugaru Strait from Honshu to Hokkaido, which implication can be partly explained by the date of the demographic expansion of BP6 species in the HSK region. Late Pleistocene population expansions (some from refugia in the glacial period) have been suggested for various mammalian species such as *Chimarrogale platycephalus* (Iwasa and Abe 2006), probably *M. fuscata* (Kawamoto et al. 2007), *Petaurista leucogenys* (Oshida et al. 2009b), probably *Meles anakuma* (Tashima et al. 2011), and *Capricornis crispus* (see Appendix). It would have been too late for these species to move across the Tsugaru Strait. An alternative explanation for the absence of BP6 species in Hokkaido, based on environmental filtering, is discussed in Sect. 3.4.2.

On the other hand, as in the case of the oldest lineages in Hokkaido [*Ochotona (O.) hyperborea* and *Myodes (M.) rex*], highly endemic lineages in the HSK region also have restricted or fragmented distributions. For example, *Glirulus japonicus*, whose divergence from the closely related European species (*Glis glis*) dates back to 24 to 30 MYA (Table 3.2) (Nunome et al. 2007), has nine highly fragmented populations in the HSK region. These populations are believed to have diverged 3 to 5 MYA in the Pliocene (Table 3.2) (Yasuda et al. 2007, 2012). Among species with Early Pliocene origins, *Euroscaptor mizura* is restricted to montane regions, and *Mogera tokudae* and *Mogera etigo*, constituting an old lineage among the BP6 species, are confined to Sado Island and the Echigo Plain, respectively. The trend of high levels of endemism, restricted distributions, and absence in Hokkaido among these old lineages cannot be explained by geological processes. The alternative explanations of competitive interactions and environmental filtering are discussed in Sect. 3.4.2.

Of the six BP4 species distributed in both Hokkaido and the HSK regions, five (*Vulpes vulpes*, *Ursus arctos*, *Mustela erminea*, *Mustela nivalis*, and *Cervus nippon*) appear to have had multiple origins, that is, several independent migrations from the continent (Table 3.2; see Appendix). Most estimated dates of origin for BP4 species are in the Middle Pleistocene (on average, the data indicate that *V. vulpes* originated in the Early Pleistocene) (Table 3.2). It is not certain whether *V. vulpes* migrated from the north, south, or both; however, it is clear that *U. arctos*, *M. erminea*, and *M. nivalis* migrated from the north because of the current northerly distributions of these species and their close relatives.

For the foregoing species, some lineages that colonized earlier could have migrated into the HSK region, whereas those that migrated later would have been blocked by the Tsugaru Strait in the Late Pleistocene. In contrast, *Cervus (C.) nippon* may have migrated through the southern route, as its close continental relatives have a largely southern distribution in China. Nagata et al. (1999) indicated that the divergence between northern and southern lineages of *C. nippon* in Japan occurred before the divergence between the Japanese and continental lineages, and estimated that the Japanese lineages were formed by multiple migrations around 0.3 MYA. This time estimate is consistent with the presence of land bridges across both the Tsugaru and Korea (Tsushima) Straits in the Middle Pleistocene, explaining the present distribution of *C. nippon* on all the major islands of Japan.

Apodemus speciosus and *Apodemus argenteus* have similar distributions in the Hokkaido and HSK regions, although they are endemic to the Japanese Archipelago (BP5). Their origins are estimated to be in the Late Miocene, although the first divergence in each species occurred much more recently in the Middle Pleistocene (see MRCA dates) (Fig. 3.2) (Suzuki et al. 2003, 2004, 2008; Tomozawa and Suzuki 2008). Therefore, it is conceivable that both *Apodemus* species may have colonized Hokkaido no later than the Middle Pleistocene, when the Tsugaru Strait land bridge was formed.

As for the BP7 species, 2 species (*Mogera wogura* and *Ursus thibetanus*) appear to have originated around 1.2 MYA, in the Early Pleistocene (Fig. 3.2), as is similar to the 14 BP6 species that also have origins in the Early Pleistocene, implying species-level divergence of the Japanese lineages of *M. wogura* and *U. thibetanus*. Thus, the BP7 and BP6 species in Japan have similar levels of endemism. This time scale is consistent with the geological evidence presented by Ohshima (1991), which shows that the Korea (Tsushima) Strait was a feasible route of dispersal in the Middle Pleistocene and earlier.

One subspecies of *Sus scrofa leucomystax* (BP8) has a distribution similar to that of the BP7 species, albeit with a slightly more recent origin (the Middle Pleistocene) (Table 3.2, Fig. 3.2). Nevertheless, the estimated date of origin is still consistent with geological evidence for the availability of the Korea (Tsushima) Strait as a dispersal route. On the other hand, the BP7 species *Micromys minutus* has a Late Pleistocene origin (Table 3.2, Fig. 3.2), drastically different from that of the other BP7 species (*Mogera wogura* and *Ursus thibetanus*). There were probably no land bridges over the Korea (Tsushima) Strait in the Late Pleistocene (Ohshima 1991). Therefore, the Late Pleistocene origin of *M. minutus* requires explanation.

During the last glacial maximum (LGM) in the Late Pleistocene, the Korea (Tsushima) Strait is believed to have been a narrow seaway (~20 km across) because the sea level was 130 m lower than that of today (Park et al. 2000). Therefore, I speculate *M. minutus* may have been established in Japan after dispersal across the sea. Most of the distribution of West Indian vertebrates on the Antilles can be explained only by dispersal on floating islands composed of plants (Hedges 2006; Sato et al. 2016). *Micromys minutus* may have been dispersed by similar means: it is ecologically reliant on herbaceous plants, and sometimes nests on the floodplains of nearby rivers (Hata 2011).

The Ryukyu-endemic BP9 species exhibit a high degree of endemism (Table 3.2, Fig. 3.2), and three of five BP9 species have origins in the Late Miocene, although the precise phylogenetic relationships of *Crocidura orii* and *Pentalagus furnessi* remain to be determined (Matthee et al. 2004; Dubey et al. 2008). The genus *Tokudaia*, which diverged from the genus *Apodemus* (Sato and Suzuki 2004), has a similar extent of endemism (Table 3.2, Fig. 3.2). The divergences among three *Tokudaia* species in Amami-Oshima, Tokunoshima, and Okinawajima are estimated to have occurred at 2.58 to 1.13 MYA (see Appendix), which is consistent with the origins of *Crocidura watasei* and *Diplothrix legata* (Table 3.2, Fig. 3.2). Kimura (2000) suggested that the Ryukyu Islands were connected to the Eurasian continent by land bridges multiple times in two stages, 1.6–1.3 MYA and 0.2–0.025 MYA, the former of which fits the dates of divergence estimated above. However, for the Ryukyu-endemic subspecies of *Sus scrofa riukiuanus* that is estimated to have originated in the early Middle Pleistocene (<0.66 MYA) (Table 3.2, Fig. 3.2), we should expect to find a closely related (still unidentified) lineage on the continent: fossil evidence suggests that the wild boar is likely to have migrated into the Ryukyu Islands 0.018 MYA (Hasegawa 1980), which is largely consistent with the geology of the Ryukyu Islands (Kimura 2000).

Among the BP10 species inhabiting the small islands adjacent to the main Japanese islands and the Eurasian continent, two of three species in the Tsushima Islands (*Crocidura shantungensis* and *Prionailurus bengalensis*) have Late Pleistocene origins (Table 3.2, Fig. 3.2), implying that there may have been a period when the Tsushima Islands were connected to the Eurasian continent while the Kyushu region was separated. However, the sea is deeper between Tsushima and the continent than between Tsushima and Kyushu (Park et al. 2000), which casts doubt on the land bridge hypothesis. Alternatively, these species may have been dispersed by floating land rafts (as in the case of *Micromys minutus*), although the possibility is uncertain. I discuss the role of community ecology in Sect. 3.4.2.

Mustela sibirica has a relatively ancient origin, in the Middle Pleistocene. Thus, again, an explanation other than the geological division in the Korea (Tsushima) Strait is needed for the absence of this species in the main Japanese islands (except for descendants of introduced individuals; see Sect. 3.4.2). The Iriomote leopard cat *Prionailurus bengalensis iriomotensis*, on Iriomotejima Island, diverged 0.265 MYA from its related continental lineage; this may be explained by Kimura (2000), who presented geological evidence that the Ryukyu Islands were connected to the Eurasian continent 0.2 to 0.025 MYA (in the latter of two stages of connection).

3.4.2 Ecological and Phylogenetic Explanations for the Mammalian Species Assembly in Japan

How can we explain the mammalian species distribution patterns that cannot be explained by past geological events? For example, why do mammals that are endemic to Hokkaido and have origins in the Middle Pleistocene or earlier seem not to have migrated into Honshu and the more southern regions (i.e., via land bridges in the Tsugaru Strait formed in the Middle Pleistocene or earlier) (*Sorex caecutiens*, *Sorex unguiculatus*, *Sciurus vulgaris*, *Tamias sibiricus*, *Pteromys volans*, *Myodes rufocanus*, *Myodes rex*, *Lepus timidus*, *Ochotona hyperborea*)? Why did some mammals establish lineages in the Tsushima Islands, but apparently not migrate to the main Japanese islands (*Crocidura shantungensis*, *Prionailurus bengalensis euptilurus*, *Mustela sibirica*)? Furthermore, why are HSK-endemic species derived from the southern route in the Middle Pleistocene or earlier not observed in Hokkaido, despite the fact that land bridges across the Tsugaru Strait existed during this time (many BP6 and BP7 species)?

Here, I discuss ecological and phylogenetic factors for the presence or absence of mammals in the Japanese Archipelago. As mentioned in Sect. 3.1, the coexistence of species depends on the presence of niche differences, which tend to develop when two lineages have been phylogenetically separated for a long period of time (species assortment) (Dayan and Simberloff 2005; Emerson and Gillespie 2008). Theories of coexistence are currently undergoing revision based on new molecular phylogenetics data (Narwani et al. 2015). It is therefore an opportune time to discuss the mammalian faunal assembly in Japan in light of these new molecular phylogenetic data and the coexistence theory. (It should be noted here that I use the term "coexistence" in a broad sense; "coexisting species" do not necessarily have completely overlapping habitats, and may segregate their niches in space and time by means of micro-environments.)

3.4.2.1 Biotic Influence on Mammalian Distributions

First, I discuss the distribution patterns and phylogenetic relatedness of the *Myodes* species. In Hokkaido, three *Myodes* species coexist: *M. rutilus* and *M. rufocanus* are found within the entire Hokkaido region, whereas *M. rex* has a restricted distribution, as already described (Ohdachi et al. 2015). This pattern of coexistence can be explained by species assortment between *M. rutilus* and *M. rufocanus* and competition between *M. rex* and *M. rufocanus*.

Among these three species, *M. rex* and *M. rufocanus* are the most closely related to each other, whereas *M. rutilus* is more distantly related to both (Luo et al. 2004; Lebedev et al. 2007; Kohli et al. 2014). Considering phylogenetic relatedness, if *M. rutilus* migrated into Honshu from Hokkaido, it may have coexisted with the *M. andersoni*–*M. smithii* complex, because both lineages have the same level of divergence as exists between *M. rutilus* and the lineage of *M. rex*–*M. rufocanus*

(Cook et al. 2004; Luo et al. 2004; Lebedev et al. 2007; Kohli et al. 2014). However, migration of *M. rutilus* is likely to have been blocked by the Tsugaru Strait, because the origin of this species in Hokkaido was in the Late Pleistocene (Table 3.2, Fig. 3.2). In contrast, *M. rex* and *M. rufocanus* originated in the Early and Middle Pleistocene, respectively. The clade of *M. rex* and *M. rufocanus* is more closely related to the *M. andersoni–M. smithii* complex than *M. rutilus* (Cook et al. 2004; Luo et al. 2004; Lebedev et al. 2007; Kohli et al. 2014). Based on their dates of origin, the former two species may have colonized Honshu from Hokkaido [but recent population expansion in the Late Pleistocene is also suggested for *M. rufocanus* (see Appendix)]; however, the closely related *M. andersoni–M. smithii* complex may have prevented such colonization by competitive exclusion.

Similarly, there should have been competitive interactions between closely related congeneric species pairs in Hokkaido and the HSK islands: *Sorex caecutiens* and *S. shinto* [although a population expansion of *S. caecutiens* in Hokkaido in the Late Pleistocene is also probable (see Appendix)] (Ohdachi et al. 2001); *Sciurus vulgaris* and *S. lis* (Herron et al. 2004); *Pteromys volans* and *P. momonga* (Herron et al. 2004); and *Lepus timidus* and *L. brachyurus* (Yamada et al. 2002). These pairs would likely have had similar niches, and each of the latter species endemic to the HSK islands is estimated to have been present there in the Early to Middle Pleistocene period, earlier than the migration date of the former species endemic to Hokkaido (Table 3.2, Fig. 3.2). Thus, "competitive dominance of residents" may have been a factor explaining the absence of Hokkaido-endemic species with Middle Pleistocene origins in Honshu and islands further south. However, this hypothesis cannot explain the absence of *Sorex unguiculatus*, *Tamias sibiricus*, and *Ochotona hyperborea*, which have no close relatives in Honshu and more southern islands (see Sect. 3.4.2.2).

One of three lineages of *Ursus arctos* has a date of origin in the Middle Pleistocene (Hirata et al. 2013), and paleontological evidence also supports the existence of this species in Honshu during the Pleistocene (Kawamura et al. 1989; Kawamura 1994). The fact that *U. arctos* eventually became extinct in Honshu may imply the competitive dominance of the congeneric resident species, *U. thibetanus*, in Honshu and more southern islands.

Similar explanations are possible for species that migrated to Japan using the southern route. In the case of *Crocidura shantungensis*, if it was possible to migrate to the Tsushima Islands from the Eurasian continent, it would probably also have been possible to reach Kyushu. However, the presence of other *Crocidura* species in Honshu (*C. dsinezumi*) and the Ryukyu Islands (*C. watasei* and *C. orii*) may have prevented colonization by competitive exclusion. Similarly, in the case of *Mustela sibirica* in the Tsushima Islands, a congeneric species (*M. itatsi*) would already have been present in the HSK region before the Middle Pleistocene (the time of origin for *M. sibirica* in Tsushima). In these two cases, the failure of new migrants to establish resident populations may be explained by the competitive dominance of earlier residents.

On the other hand, it is unclear why there are currently no Felidae species on the major islands of Japan (with the exception of the domestic cat, *Felis catus*). The

Japanese Archipelago may not be environmentally suitable for Felidae species (environmental filtering; Kraft et al. 2015; Sect. 3.4.2.2), or similar niches may already have been occupied by other carnivores in Japan. The number of carnivoran species tends to be small on small islands (Millien-Parra and Jaeger 1999), suggesting that the available niche space for carnivores becomes limited by the existence of multiple carnivores on islands. This idea may explain the absence of *Prionailurus bengalensis euptilurus* in the main Japanese islands. However, it should be noted that this theory is only speculative.

The opposite exclusion process, "competitive dominance of migrants," can also be found among the mammals in the Japanese Archipelago. Consider the case of *Myodes rex* and *M. rufocanus*, which are the closest living relatives to one another (Abramson et al. 2012). The former is the earlier resident, but the latter has a more widespread distribution, which implies that the later colonist (*M. rufocanus*) is competitively dominant over the earlier resident (*M. rex*). As briefly mentioned in Sect. 3.4.1, the absence of the *M. andersoni–M. smithii* complex and *Martes melampus* from Hokkaido could also be explained by the competitive dominance of migrants (*Myodes rex–M. rufocanus* and *Martes zibellina*, respectively). Similarly, among talpids, the distributions of the earlier colonists in the HSK region are restricted largely to montane regions (*Euroscaptor mizura*), islands and small areas (*Mogera tokudae–M. etigo*), and the northeastern regions (*M. imaizumi*). It has been suggested that *E. mizura*, *M. tokudae–M. etigo*, *M. imaizumi*, and *M. wogura* migrated into the Japanese Archipelago via the southern route in this order (Tsuchiya et al. 2000; Shinohara et al. 2003, 2004, 2005, 2014; Kirihara et al. 2013). The earlier colonist would have been forced to move northeastward and would eventually have been restricted in distribution by the overlap in niche with the later talpid colonists. Although more phylogeographic studies are needed, the patchy montane distribution of *Dymecodon pilirostris* and greater prevalence of *Urotrichus talpoides* may imply that the former resident was expelled by the later migrant.

It should be noted here that readers may be concerned about apparently arbitrary explanations regarding the competitive dominance of earlier residents or later migrants. For example, I proposed that the *Myodes andersoni–M. smithii* complex was competitively dominant over the later migrants *M. rufocanus* and *M. rex* in HSK, while also speculating that the later migrants *M. rufocanus* and *M. rex* were dominant over the existing *M. andersoni–M. smithii* complex in Hokkaido. These explanations may appear to conflict. However, I believe that the degree to which HSK has been isolated from the continent has tended to favor the dominance of residents (although not exclusively, because colonists appear to be dominant among talpids). In contrast, Hokkaido received migrants from the continent more frequently, so that the dominance of residents occurred to a lesser degree.

3.4.2.2 Abiotic Influences on the Distribution of Japanese Mammals

To explain distribution patterns that cannot be accounted for by biotic factors, we must consider abiotic variables. For example, the absence of *Tamias sibiricus* and *Ochotona hyperborea* in Honshu and more southerly islands may be attributable to environmental filtering (Kraft et al. 2015), because both species have peculiar ecological features in Hokkaido (they are the only ground squirrel and the only alpine lagomorph in Japan, respectively). The habitat requirements of either species may not be met by the abiotic environment in Honshu.

I am unable to explain the absence of *Sorex unguiculatus* in Honshu and more southerly islands by invoking either biotic or abiotic factors. This species has a Middle Pleistocene origin in Hokkaido and, similar to *T. sibiricus* and *O. hyperborea*, has no close competitive relatives in Honshu. Furthermore, because other shrew species exist in Honshu, the environment is not unsuitable for shrews. Because the date of this species origin is estimated to be 0.15 MYA (i.e., at the end of the Middle Pleistocene; see Appendix) and no genetic differentiation is observed between the Hokkaido and continental populations (Ohdachi et al. 2001), it is likely that the estimate is erroneous, and that the geological barrier of the Tsugaru Strait, rather than ecological and environmental mechanisms, had a more deterministic role in this species distribution.

Patchy distributions cannot always be explained by biotic forces (e.g., competitive dominance of migrants). For example, no competitive relative of *Ochotona hyperborea* seems to have migrated into Hokkaido. In this case, abiotic forces such as climate fluctuations during glacial and non-glacial periods in the Pleistocene may explain the isolated alpine distribution of this species. Similarly, *Glirulus japonicus* has the most ancient origin of Japanese mammals, and no close relatives occupy similar niches (the closest relative in Japan is the sciurid lineage, which diverged 50 to 55 MYA) (Nunome et al. 2007). The long existence of *G. japonicus* in the Japanese Archipelago implies that the species survived the glacial–non-glacial cycles in the Pleistocene, which is strange, because dormice generally favor warm forest environments. It is likely that the hibernation strategy of this species allowed the persistence of each local lineage in Japan without extensive shifts in distribution during unfavorable glacial phases.

It is also unclear why HSK-endemic species derived from the southern route in the Middle Pleistocene or earlier did not reach Hokkaido despite the presence of land bridges across the Tsugaru Strait during this period. One reason may be the Late Pleistocene population expansion in HSK, as explained in Sect. 3.4.1. Because, in most cases, no closely related species are found in Hokkaido (e.g., talpids, *G. japonicus*, or *Microtus montebelli*), environmental filtering may be the most plausible explanation for the absence of HSK-endemic species in Hokkaido. The soil in Hokkaido may not fit the requirements of talpids; similarly, the climate may be too harsh (too cold) for *G. japonicus*. In any case, further ecological studies are needed for each species.

3.4.2.3 Coexistence by Species Assortment

In addition to the processes of competitive exclusion and environmental filtering, species assortment may have contributed to the distribution of Japanese mammals. Through species assortment, communities tend to comprise ecologically well-differentiated species. For example, sciurid species from different genera coexist in Hokkaido (*Pteromys volans*, *Sciurus vulgalis*, and *Tamias sibiricus*) and HSK (*Pteromys momonga*, *Sciurus lis*, and *Petaurista leucogenys*). These genera have three different modes of locomotion: gliding (*Pteromys* and *Petaurista*), arboreal (*Sciurus*), and terrestrial (*Tamias*), which helps to segregate their niche space within ecological communities. These genera are estimated to have diverged in the Oligocene to the Early Miocene (Mercer and Roth 2003), so they are also phylogenetically well separated. Similarly, three mustelid taxa endemic to the HSK region (*Martes melampus*, *Mustela itatsi*, and *Meles anakuma*) coexist and have different ecological lifestyles (terrestrial, arboreal, and fossorial, respectively). They are assigned to different subfamilies (Guloninae, Mustelinae, and Melinae, respectively) (Sato et al. 2012; Sato 2016; Sato and Wolsan 2016), and are estimated to have diverged from one another in the Middle to Late Miocene (Sato et al. 2009, 2012).

Even within the same genus, niche segregation can make coexistence possible. Two carnivorous *Mustela* species, *M. nivalis* and *M. erminea*, widely coexist in the Holarctic region. These species diverged 3.5 to 4.0 MYA (Sato et al. 2012), and it has been suggested that their coexistence is maintained through resource partitioning (Sato 2013). The *Apodemus* species provide another potential example of species assortment within a genus. In Japan, two species coexist in the HSK region (*A. argenteus* and *A. speciosus*), and three in Hokkaido (*A. argenteus*, *A. speciosus*, and *A. peninsulae*). There are four major lineages in the genus *Apodemus*: the *argenteus*, *gurkha*, Asian (*A. speciosus* and *A. peninsulae* are included), and European lineages. *A. argenteus* and *A. speciosus* are among the major lineages that diverged 7.3 MYA, and, within the Asian lineage, *A. speciosus* is the most divergent species, having diverged from the lineage that includes *A. peninsulae* 5.9 MYA (Suzuki et al. 2008). Based on these results, and those for other *Apodemus* species (mainly in East Asia), Suzuki et al. (2003, 2008) suggested that *Apodemus* species belonging to different major lineages could coexist in the same habitat; this is considered to be a type of species assortment. However, the ecological niche differences that enable coexistence among *Apodemus* species are not clear, and further research on the ecological traits of each species is required.

The previously described coexistence between *Myodes rutilus* and *M. rufocanus* may also be a result of species assortment, although the divergence between them is estimated to be more recent (1.8–4.0 MYA) (Luo et al. 2004; Lebedev et al. 2007; Kohli et al. 2014). However, what about *Sorex* species? The divergence among the four lineages (*caecutiens-shinto*, *unguiculatus-isodon*, *minutissimus-hosonoi*, and *gracillimus*) is estimated to have occurred 0.9 MYA based on the data of Ohdachi et al. (2001), where the average sequence divergence, 9.9 %, was divided by the 11 %/million year divergence rate of Hope et al. (2010). The *Sorex* species have the most recent date of divergence among all coexisting species in the literature I reviewed.

Other instances of coexistence within a family can also be easily accounted for by the species assortment of phylogenetically (and therefore probably ecologically) well-differentiated species (Soricinae and Crocidurinae species, *Chimarrogale platycephalus* and the *Sorex* species, *Micromys minutus* and the *Apodemus* species, *Diplothrix legata* and the *Tokudaia* species, *Microtus montebelli* and the *Myodes* species, and *Vulpes vulpes* and *Nyctereutes procyonoides*). In summary, a certain degree of phylogenetic distance is required for the coexistence of mammals in the Japanese Archipelago. For non-volant and nonintroduced terrestrial mammals, there are no coexisting species pairs that diverged in the Middle Pleistocene or later.

3.5 Conclusion

In this review, I have discussed the contribution of four main factors to the composition of Japanese mammals. First, the geological vicariance events in the Tsugaru and Korea (Tsushima) Straits were certainly important factors. Second, competitive exclusion processes related to phylogenetic proximity can explain some of the patterns of presence and absence among Japanese mammals. Third, abiotic environmental filtering can explain some patterns in mammal distribution that cannot be explained by geological and biotic influences. Fourth, species assortment can lead to the coexistence of phylogenetically distant (and therefore probably ecologically dissimilar) species in the Japanese Archipelago. Thus, it can be concluded, on the basis of modern chronological data from molecular phylogenetic and phylogeographic studies, that geological, ecological, and phylogenetic factors concertedly and species-dependently determined the Japanese mammalian faunal assembly.

It should be stressed that the majority of the mammalian faunal assembly can be explained by geological and community ecological mechanisms in the Japanese Archipelago. Future studies may be able to achieve more reliable time estimates for the divergence and demographic expansion of Japanese mammals, more comprehensive sampling of both continental and Japanese species (or lineages), and more precise dating with genome-scale data and sophisticated dating methodologies (taking into consideration the evolutionary rate differences mentioned earlier and using robust fossil calibration points). Furthermore, phylogenetic dispersion is not necessarily correlated with ecological niche distance (Gerhold et al. 2015). Therefore, more research on the precise ecological niche of each mammal will allow instances of competitive exclusion and environmental filtering to be more reliably identified. Such research may include ecomorphological analyses of organisms within the same guild (Werdelin and Wesley-Hunt 2010), as well as computer modeling (e.g., species distribution modeling analyses) (Svenning et al. 2011). Exploring these avenues for further research will enhance our understanding of the underlying mechanisms for the distributions of Japanese mammals.

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Appendix

Here, I have reviewed molecular phylogenetic and phylogeographic studies of Japanese mammals to obtain reliable estimates of the divergence time between the Japanese and the continental species (or lineage) and the time to the most recent common ancestor (MRCA) of the Japanese mammals. Where no chronological data were provided in the previous study, even though some DNA sequences were determined and available in the DNA database, I briefly calculated these times by using the lineage-specific evolutionary rate. It should be noted here that the most commonly used evolutionary rates proposed by Brown et al. (1979) and Irwin et al. (1991) were not considered effective because the former was based on only the restriction fragment-length polymorphisms (RFLP), which provide less sufficient variations than the sequence data (McKay 2012 used this rate), and both rates were estimated from a limited mammalian group (primates in the former and ungulates in the latter; McKay 2012 applied this rate to all the mammalian lineage divergence), so that the applications of these rates to other groups would be difficult because of the differences in the evolutionary rates among mammalian groups. For example, a corollary of the application of the evolutionary rate obtained from a slowly evolving lineage (e.g., ungulates) into a rapidly evolving lineage (e.g., rodents) is an overestimation of the divergence times on the rapidly evolving lineage.

Eulipotyphla

Soricidae

Soricidae is the most speciose insectivorous family in the order Eulipotyphla and includes 26 genera and 376 species distributed worldwide (Hutterer 2005). These species could be classified into two subfamilies, Soricinae and Crocidurinae (Dubey et al. 2007; but Myosoricinae was proposed as the third subfamily by Hutterer 2005). In a molecular phylogenetic study with two mitochondrial (*Cytb* and *16S rRNA*) and two nuclear (*Apob* and *Brca1*) genes, these subfamilies were demonstrated to have diverged in the late Early Miocene [ca. 20 MYA (million years ago) (Fumagalli et al. 1999; Dubey et al. 2007)]. In the Japanese Archipelago, seven soricine (six *Sorex* and one *Chimarrogale*) and five crocidurine (four *Crocidura* and one *Suncus*) species exist (Ohdachi et al. 2015). As regarding *Sorex* species in the subfamily Soricinae, four of six species (*S. minutissimus*, *S. caecutiens*, *S. unguiculatus*, and *S. gracillimus*) have a similar distribution across the northern Eurasian continent and eastern marginal islands including Hokkaido, Sakhalin, and adjacent small islands [not present in the Honshu–Shikoku–Kyushu (hereafter designated as HSK) and Ryukyu regions], representing BP2 (Table 3.1). The other two *Sorex* species (*S. hosonoi* and *S. shinto*) are both endemic to the HSK region (BP6; Table 3.1) and are phylogenetically close to *S. minutissimus* and *S. caecutiens*, respectively (Ohdachi et al. 1997, 2001, 2006). This phylogenetic structure suggests that the generations of *S. hosonoi* and *S. shinto* lienages were earlier than those of the Hokkaido lineage of each sister species, *S. minutissimus* and *S. caecutiens*, respecitively. It could therefore be assumed that *S. hosonoi* and *S. shinto* were earlier colonizers of the Japanese archipelago than *S. minutissimus* and *S. caecutiens*, respectively. Ohdachi et al. (2001) examined intraspecific genetic variations based on the *Cytb* gene for all the six Japanese *Sorex* species and found that, despite the similarity in the distribution patterns of the four Palaearctic *Sorex* species (*S. caecutiens*, *S. minutissimus*, *S. unguiculatus*, and *S. gracillimus*), their phylogeographic patterns are different from each other; where the Hokkaido lineage of *S. caecutiens* is well differentiated from the continental one, no genetic differentiations are observed between Hokkaido and the continental populations in *S. minutissimus* and *S. unguiculatus*, and there are three distinct haplogroups specific to the Hokkaido population of *S. gracillimus*. These observations suggest that the four *Sorex* species in Hokkaido established their lineages by different histories in spite of the similar distribution patterns. However, in Ohdachi et al. (2001), the time scale for the lineage differentiations was not assessed based on their molecular data. Hope et al. (2010) estimated that the mutation rate/lineage/myr for the *Cytb* gene in the *S. minutissimus* lineage was 5.5 % (therefore 11 % divergence rate/myr), assuming 1 MYA for the divergence between *S. hosonoi* and *S. minutissimus* on the basis of the geological evidence, and obtained the result that the time to the most recent common ancestor (MRCA) of lineages in *S. minutissimus* including the Hokkaido linage was in the period of the Late Pleistocene (<0.13 MYA). This time estimate is in agreement with the distribution pattern of *S. minutissimus* in Japan, that is, absence from HSK and Ryukyu regions that would have been caused by the Tsugaru Strait established in the Late Pleistocene, preventing the dispersals from Hokkaido to the southern major islands of Japan (Ohshima 1991).

Here, I adopt the evolutionary rate of Hope et al. (2010) for the data of Ohdachi et al. (2001) to introduce the time scale into the Japanese *Sorex* species evolution. However, because the evolutionary rate of Hope et al. (2010) was based on the divergence between *S. hosonoi* and *S. minutissimus* resulting from the geological features of the Japanese Archipelago, the application of this rate to test the influence of the straits around the Japanese Archipelago on the genetic diversity of Japanese *Sorex* species might have fallen into circular argument. Nevertheless, a similar evolutionary rate was suggested to be fit to the late Quaternary phylogeography of various taxa from rodents to carnivorans around the Bering Straits (Hope et al. 2014). Therefore, I used the 11 %/myr (million years) divergence rate in this tentative time estimations. The average pairwise genetic distances between species endemic to the HSK region (*S. hosonoi* and *S. shinto*) and each sister species (*S. minutissimus* and *S. caecutien*s, respectively) were calculated to be 8.3 % and 8.8 %, respectively, thus suggesting that these lineages diverged 0.75 and 0.8 MYA in the Early to Middle Pleistocene, respectively. On the other hand, Hokkaido lineages of *S. minutissimus* and *S. caecutien*s were estimated to have diverged

0.07 and 0.56 MYA, respectively. It is obvious to obtain the age estimate consistent with Hope et al. (2010) for *S. minutissimus* because of the same assumption about the evolutionary rate. However, the Middle Pleistocene origin of the Hokkaido lineage of *S. caecutiens* provides a novel insight (Ohdachi et al. 2001 assumed the early Late Pleistocene origin), although the most divergent lineages in Hokkaido in *S. caecutiens* was inferred to have split 0.09 MYA, implying that the lineage diversifications in Hokkaido might have occurred in the Late Pleistocene. Meanwhile, it was estimated that *S. unguiculatus* diverged from the most closely related species, *S. isodon*, 0.64 MYA. There is no genetic differentiation between the Japanese and continental populations in *S. unguiculatus*, where the average pairwise distance between Khabarovsk and Hokkaido haplotypes and that among the Hokkaido haplotypes both show 1.6 % corresponding to 0.15 MYA based on the 11 %/myr divergence rate, suggesting that the Hokkaido lineage diverged from the continental one in the final part of the Middle Pleistocene. Regarding *S. gracillimus*, it was calculated that the divergence between the Hokkaido and the continental lineages, that among three haplogroups in Hokkaido, and that within each of the three haplogroups, occurred 0.07, 0.05, and 0.02 MYA, respectively. All the events took place in the Late Pleistocene. The foregoing calculation suggests that the absence of *S. minutissimus* and *S. gracillimus* in Honshu and more southern islands can be explained by the barrier of the Tsugaru Strait in the Late Pleistocene (Ohshima 1991). It is not clear why *S. caecutiens* and *S. unguiculatus*, whose origin in Hokkaido is in the Middle Pleistocene, did not cross the Tsugaru Strait, when the land bridge was formed. Probably, the lineage expansion would have occurred in the Late Pleistocene, as suggested in *S. caecutiens*, or some community ecological mechanisms might have been applied (see Sect. 3.4.2 in the text).

The other soricine species, the Japanese water shrew *Chimarrogale platycephalus*, is a semiaquatic species endemic to the HSK region (BP6; Table 3.1) (the scientific name was used following Ohdachi et al. 2015). He et al. (2010) intensively examined the interspecific phylogenetic relationships among shrew species representing all the genera within the tribe Nectogalini, where *Chimarrogale* is included, based on eight mitochondrial genes (*Cytb*, *Co1*, *Atp6*, *Nd2*, *Nd4*, *Nd5*, and *12S* and *16S rRNA*) and three nuclear protein-coding genes (*Apob*, *Brca1*, and *Rag2*). They showed that two semi-aquatic *Chimarrogale* species, *C. platycephalus* and *C. himalayica*, were closely related to each other, and estimated the divergence time between them on the basis of the two nuclear protein-coding genes (*Apob* and *Brca1*) to be 1.25 MYA with several assumptions of fossil calibrations (the oldest remain of the Soricinae–Crocidurinae ancestor at 20 MYA, the oldest Blarinellini and Blarinini at 15 MYA, and the oldest known fossil species of the subgenus *Sorex* at 3.5 MYA). However, special caution must be given to the interpretation of their results. First, *C. platycephalus* in their study is designated to be of Taiwan origin (see their Table 3.1), which is not consistent with the current taxonomy because *C. platycephalus* is endemic to Japan. Second, because *C. himalayica* in their study is designated to be of Yunnan origin, the foregoing time estimate should be viewed as the divergence time between Taiwanese and continental lineages of *C. himalayica*. Ohdachi et al. (2006) and Yuan et al. (2013) showed that *C. platycephalus* is more closely related to *C. himalayica* in Taiwan than is the continental *C. himalayica*, suggesting that *C. himalayica* is paraphyletic to *C. platycephalus*. Yuan et al. (2013), using the *Cytb* gene, estimated the branching time of *C. platycephalus* to be 3.03 MYA. However, this is possibly overestimated because of the use of the *Cytb* gene whose substitutions would be saturated in the time scale of their study, where the calibration point was set to approximately 20 MYA, that is, at a level subjected to the saturation problem (Steppan et al. 2005). Although He et al. (2010) adopted an incorrect taxonomic framework for *C. platycephalus*, I suppose that their time estimates could be more realistic because they estimated divergence times by less-saturated nuclear protein-coding genes and obtained dates largely concordant with the fossil records (He et al. 2010). Taking into account that Yuan et al. (2013) estimated the divergence time between Taiwanese and continental lineages of *C. himalayica* to be 4.58 MYA and He et al. (2010) estimated 1.25 MYA, as already explained, 3.03 MYA estimated for the split between *C. platycephalus* and *C. himalayica* in Taiwan in Yuan et al. (2013) could correspond to age about 0.83 MYA by a very brief proportion calculation. Furthermore, Yuan et al. (2013) indicated that the genetic distance of the *Cytb* gene between *C. platycephalus* and *C. himalayica* in Taiwan is 10.5 %. If I use the 11 %/myr of Hope et al. (2010), the time estimate for this divergence would be 0.95 MYA, which is close to 0.83 MYA, although slightly larger.

Based on the mitochondrial *Cytb* variations of *C. platycephalus*, Iwasa and Abe (2006) clarified that there are four geographically separated phylogroups in the Japanese archipelago, one in Kyushu and the other three in Honshu. The most southern Kyushu lineage first diverged, then the Chugoku lineage in the southwestern Honshu, and in the last Kinki lineage in the east of the Chugoku region and the lineage in East and Central Honshu were separated. The time to the MRCA of the four phylogroups was inferred to be 0.39 MYA, and divergence in each phylogroup was estimated to have occurred within 0.059 MYA, on the basis of the 1.36 % transversional susbtitutions at the third codon positions per million years calculated from setting the divergence time between Soricinae and Crocidurinae to be 20 MYA, according to Fumagali et al. (1999), in which the transversional susbtitutions at the third codon positions was checked to be not saturated. In addition, by using the 11 %/myr of Hope et al. (2010) for the data of Iwasa and Abe (2006) where average pairwise genetic distances between haplotypes in Kyushu and East-Central clades is 3.0 %, the divergence time was calculated to be 0.27 MYA, which is not inconsistent with the Middle Pleistocene origin of *C. platycephalus* as estimated earlier (0.39 MYA). All these inferences suggest that *C. platycephalus* originated in the southern part of the Japanese Archipelago (except for the Ryukyu region) in the Middle Pleistocene and expanded northward from four different refugia in a post-glacial period in the Late Pleistocene (Iwasa and Abe 2006). As already described, because the Tsugaru Strait was not considered to have had a land bridge in the Late Pleistocene, the absence of this species from Hokkaido can be explained by the Late Pleistocene expansion of the Honshu lineages from each refugium. The reason for the absence of this species from the Shikoku islands is not clear.

Of all the five Crocidurinae shrew species in the Japanese archipelago, only one species, the Japanese white-toothed shrew *Crocidura dsinezumi*, is endemic to the HSK region (BP6), whereas the others are restricted to small islands around the Japanese archipelago, especially in the Ryukyu region: the Orii's shrew *C. orii* (Amami Isl., BP9; Table 3.1), the Asian lesser white-toothed shrew *C. shantungensis* (Tsushima Isl., BP10; Table 3.1), the Watase's shrew *C. watasei* (Amami and Okinawa Isl., BP9; Table 3.1), and the musk shrew *Suncus murinus* (Amami, Okinawa, Miyako, and Yaeyama Isl., BP10; Table 3.1). Dubey et al. (2008) examined the phylogenetic relationships among *Crocidura* and *Suncus* species with two mitochondrial (*Cytb* and *16S rRNA*) and two nuclear (*Apob* and *Brca1*) genes, and estimated that the Crocidurinae shrew species were inferred to have diversified on mainly Palaearctic and Oriental regions since the Late Miocene. One of major clades derived from the diversifications is the Asian clade, where all the four *Crocidura* species in Japan were included (Dubey et al. 2008). Using the calibration point of 20 MYA for the divergence between Soricinae and Crocidurinae, Dubey et al. (2008) estimated that *C. dsinezumi* diverged from the clade that comprised *C. lasiura* and *C. kurodai* 1.42 MYA, *C. watasei* branched from the most closely related species *C. horsfieldi* 1.11 MYA, and *C. orii*, whose phylogenetic affinity was not unambiguously inferred, was generated 5.42 MYA during the earliest diversification among the Asian clade. *C. shantungensis* is also a member of the Asian clade and has been demonstrated to be the most closely related to the *C. suaveolens* group (Ohdachi et al. 2004; Dubey et al. 2006, 2008). Although the divergence of *C. shantungensis* in Tsushima Islands has not been dated in any of these previous studies, data used by Motokawa et al. (2000) and Ohdachi et al. (2004) showed that pairwise difference of the *Cytb* gene between the Tsushima lineage and the most closely related Cheju lineage was 1.2 %, suggesting that the divergence time is 0.1 MYA on the basis of the 11 %/myr divergence rate of Hope et al. (2010). Unfortunately, the intraspecific genetic variations of *S. murinus* including the Japanese lineage have never been investigated. Thus, the time scale cannot be evaluated here. Concerning the other intraspecific genetic diversity of these Crocidurinae species, it was suggested that there is a clear phylogeographic demarcation between eastern and western Japanese lineages in *Crocidura dsinezumi* (Han et al. 2002; Ohdachi et al. 2004). Their average pairwise genetic distance is 3.7 %, indicating that evolutionary split between eastern and western linages occurred 0.34 MYA based on the 11 %/myr divergence rate. It has also been known that individuals of *C. watasei* in Amami-Oshima and Okinawajima Islands have the same *Cytb* haplotype (Motokawa et al. 2000).

Talpidae

The family Talpidae comprises 39 species and shows a variety of ecological lifestyles, including fossorial, semi-fossorial, terrestrial, and semi-aquatic insectivorous mammals (Hutterer 2005). Eight talpid species are present in Japan, of which six species are fossorial moles (five *Mogera* and one *Euroscaptor* species) and two are semi-fossorial shrew moles (one *Dymecodon* and one *Urotrichus* species). Seven of these eight talpid species are endemic to the Japanese archipelago and only *M. wogura* is also found in the eastern Eurasian continent [Hutterer 2005; this species is sometimes considered endemic to Japan because the Eurasian lineage is classified as *M. robusta* (Zemlemrova et al. 2013)]. No talpid species are observed in Hokkaido. The biogeographic patterns for the talpid species are BP6 [the lesser Japanese shrew mole *Dymecodon pilirostris*, the greater Japanese shrew mole *Urotrichus talpoides*, the Japanese mountain mole *Euroscaptor mizura*, the lesser Japanese mole *Mogera imaizumii*, and the Echigo mole Mogera etigo (the last one is considered the same species as the Sado mole Mogera tokudae); Table 3.1], BP7 (the large Japanese mole *Mogera wogura*; Table 3.1), and BP9 (the Senkaku mole *Mogera uchidai*; Table 3.1). Their precise distributions are not considered to overlap except for the narrow geographic boundaries among them. In fact, the distribution of *E. mizura* is only observed in the restricted and fragmented montane regions in Japan; *M. tokudae* and *M. etigo* are confined to Sado Islands and nearby Echigo Plain in Honshu, respectively, *M. imaizumii* is mainly observed in the eastern part of Japan and remains in very limited regions in some western parts of Japan, and *M. wogura* predominantly occupies the western part of Japan and possesses the same species as in the Eurasian continent. These distribution patterns suggest the different evolutionary history among these mole and shrew mole species. Previous molecular phylogenetic analyses have clarified that the Asian fossorial moles formed a monophyletic lineage (*Euroscaptor* and *Mogera* are included), in which, in the Japanese moles, *E. mizura* constitutes monotypic lineage that diverged in the most basal part within the Asian mole clade, and *M. imaizumii* and *M. wogura* (including Eurasian and Japanese lineages) are sister species to each other with the *M. tokudae*–*M. etigo* clade closely related to the *M. imaizumii*–*M. wogura* clade (Tsuchiya et al. 2000; Shinohara et al. 2003, 2004, 2005, 2014; Zemlemrova et al. 2013; He et al. 2014; as no molecular studies have been conducted for *M. uchidai*, I could not discuss the origin of this species hereafter). Namely, among the Japanese mole species, *E. mizura* branched off first, *M. tokudae*–*M. etigo* second, *M. imaizumii* third, and the Japanese lineage of *M. wogura* at the last. Combined with the distributions of these moles in the Japanese Archipelago, these phylogenetic relationships suggest that the Japanese mole species migrated from the Eurasian continent following the branching order in the phylogeny, implying that the earlier the migration is, the more restricted the distributions are to montane regions, islands and small areas, and the northeastern region in Honshu. On the basis of the fossil record (16.4–20.5 MYA for the earliest Talpini fossil in East Asia and 4.0–4.3 MYA for the oldest *Scaptochirus* fossil), the divergence time of the *E. mizura* lineage was estimated to be 17.1 MYA in the analyses using the mitochondrial *Cytb* and *12S rRNA* and nuclear *Rag1* genes (Shinohara et al. 2014). Shinohara et al. (2014) also inferred that the lineage of *M. tokudae* (*M. etigo* should also be placed here) was generated 8.6 MYA and that *M. imaizumii* diverged from *M. wogura* (both Eurasian and Japanese lineages are included) 5.7 MYA. On the other hand, using the similar calibration standard based on the fossil records, He et al. (2014) estimated by the 2 mitochondrial genes (*Cytb* and *12S rRNA*) and 12 nuclear genes (*Adora3*, *Atp7a*, *App*, *Bche*, *Bdnf*, *Bmi1*, *Brca1*, *Crem*, *Plcb4*, *Rag1*, *Rag2*, and *Ttn*) that the *E. mizura* lineage diverged 12.32 to 13.45 MYA and the *M. imaizumii*/*M. wogura* split occurred 3.42 to 4.5 MYA, thus indicating estimates younger than those in Shinohara et al. (2014). This difference in the time estimates would be caused by the stronger effect of the mitochondrial genes in Shinohara et al. (2014). Tsuchiya et al. (2000) also indicated similar time estimates by using the transversional substitutions of the *Cytb* gene. The results show that *E. mizura*, *M. tokudae*, and *M. imaizumii* branched off in this order 12.6–17.7, 6.6–9.2, and 2.5–3.4 MYA, respectively (Tsuchiya et al. 2000). Kirihara et al. (2013) assumed that the divergence between *Talpa europaea* and *Talpa caucasica* occurred 4.75 MYA and estimated with the *Cytb* gene that *E. mizura*, *M. tokudae*, *M. imaizumii*, and the Japanese lineage of *M. wogura* branched off in this order 5.21, 3.64, 2.31, and 1.20 MYA, respectively. These time estimates are much younger than those in other studies. I suppose that the divergence times inferred by Shinohara et al. (2014) and He et al. (2014) might be overestimates because they depended on the mitochondrial genes in some degree for the time scale, where the mitochondrial genes would not work well because of the saturation problem, and also adopted the calibration point based on the earliest record of Talpini in East Asia (16.4–20.5 MYA), which might also be too old for the mitochondrial gene variations to be calibrated. Although Tsuchiya et al. (2000) focused on less-saturated transversional substitutions, the depth of the calibration point seems too old (25–35 MYA for the divergence between Urotrichini and Talpini), so that the estimated time scale may be overestimated. The estimates of Kirihara et al. (2013) are in agreement with the geological and eustatic records and the migration ages of the proboscidean species into Japan. Kirihara et al. (2013) also suggested that the genetic distance between *M. tokudae* in Sado Islands and *M. etigo* in Echigo Plain is only 2 %, indicating that, on the basis of their divergence rate of the *Cytb* gene (4–6 %/myr), these two “species” diverged 0.3 to 0.5 MYA; this is a level of intraspecific variation (Kirihara et al. 2013).

With respect to two shrew mole species *D. pilirostris* and *U. talpoides* endemic to the Japanese Archipelago, their origins have not been clearly understood. Previous molecular phylogenetic analyses demonstrated that these two shrew mole species formed a clade (Shinohara et al. 2003, 2004). However, no time scale has been estimated yet. Furthermore, as no talpid species is closely related to one of these species (that is, the clade consists of these two species only), it is not clear which species migrated into the Japanese Archipelago first. Taking into account that *D. pilirostris* has a scattered distribution in the montane region as in the case of *E. mizura*, and *U. talpoides* occupies most lowlands of the Japanese

Archipelago similar to *Mogera* species in Japan, it might be likely that *D. pilirostris* established its lineage in Japan earlier than *U. talpoides*. A simple calculation with the 4–6 %/myr *Cytb* divergence rate for East Asian mole species (Kirihara et al. 2013) led to 1.9–2.85 MYA for the divergence time between *D. pilirostris* and *U. talpoides* (average pairwise genetic distance was 11.4 %; data were derived from Shinohara et al. 2003).

It should also be noted here that *E. mizura*, *D. pilirostris*, and *U. talpoides* show a very high extent of intraspecific variations corresponding to the interspecific difference in other mole and shrew mole species (Shinohara et al. 2003, 2014). The average pairwise genetic distances between the most divergent lineages in *E. mizura*, *D. pilirostris*, and *U. talpoides* are 7 %, 10.6 %, and 6.9 %, respectively, on the basis of the data of Shinohara et al. (2003, 2014), which could be calculated to be 1.17–1.75 MYA, 1.77–2.65 MYA, and 1.15–1.73 MYA, respectively, following a 4–6 %/myr *Cytb* divergence rate (Kirihara et al. 2013). These time estimates may correspond to the interspecific levels of diversifications.

Primates

Cercopithecidae

Cercopithecidae is the most speciose primate family, composed of 132 species of Old World monkeys (Groves 2005). Among them, only 1 species, the Japanese macaque *Macaca fuscata* endemic to Japan, can be found in the HSK region (BP6; Table 3.1). Previous molecular phylogenetic analyses with the mitochondrial or nuclear gene sequences demonstrated that *M. fuscata* is closely related to the rhesus macaque *Macaca mulatta* and the Taiwan macaque *Macaca cyclopis* (Hayasaka et al. 1996; Tosi et al. 2003; Chu et al. 2007). Assuming that the divergence between Asian and Barbary macaques occurred 3.0 MYA, based on the fossil record and using a portion of the mitochondrial DNA sequences (*Nd4*, *Nd5*, and some *tRNAs*), Hayasaka et al. (1996) estimated that *M. fuscata* diverged from the clade of *M. mulatta* and *M. cyclopis* 0.65 to 0.73 MYA and the differentiation among three Japanese lineages took place 0.19 to 0.37 MYA. On the other hand, Tosi et al. (2003) utilized the mitochondrial (*12S rRNA*, *tRNA-VAL*, and *16S rRNA*) and Y-chromosomal (*Sry* and *Tspy*) genes for the divergence time estimations postulating that the initial divergence of macaques occurred 5.5 MYA, caused by the Messinian Salinity Crisis. In this study, the time for the branching of *M. fuscata* from the other closely related species above was estimated to be 1.0 MYA in the Y-chromosomal gene tree. Although not estimated clearly, the mitochondrial gene tree suggested that *M. fuscata* diverged in a time younger than 1.2 MYA, which is consistent with the Y-chromosomal gene estimation (Tosi et al. 2003) and also is not contradicted by the estimates of Hayasaka et al. (1996; 0.65–0.73 MYA). Afterward, in a study with more extensive within-species sampling for *M. fuscata*, *M. cyclopis*, and *M. mulatta*, and on the basis of the divergence rate of 28 %/myr of the mitochondrial control region, the divergence of *M. fuscata* from the continental lineages of *M. mulatta* was estimated to be 0.38 to 0.42 MYA (Chu et al. 2007). Each of the species *M. fuscata* and *M. cyclopis* shows close affinity to one of the different lineages of *M. mulatta* (for example, *M. fuscata* is closely related to a *M. mulatta* lineage from southeastern China and Vietnam). Thus, *M. mulatta* is not monophyletic (Chu et al. 2007), and this further suggests that the lineages of *M. fuscata* and *M. cyclopis* are consequences of the dispersal of *M. mulatta* into the eastern marginal islands of the Eurasian continent. Although the exact time of the migration has not been fixed yet, the last estimate by Chu et al. (2007) is not inconsistent with the palaeontological record that the oldest fossil of *M. fuscata* was discovered in Japan around 0.43–0.63 MYA (Aimi 2002).

Marmi et al. (2004) conducted intraspecific phylogeographic and demographic analyses for *M. fuscata* by using a portion of the control region and obtained a consistent estimate for the colonization age of the ancestor of *M. fuscata* (0.31–0.88 MYA). They also showed that the extent of the genetic difference between *M. fuscata* and the eastern lineage of *M. mulatta* is less than that between eastern and western lineages of *M. mulatta* and proposed that the *M. fuscata* be included in the same species as the eastern *M. mulatta* (Marmi et al. 2004). Treating both species as a single species, they further suggested that the ancestral population of *M. fuscata* and the eastern *M. mulatta* experienced a rapid expansion 0.16 to 1.00 MYA (Marmi et al. 2004). Kawamoto et al. (2007) similarly examined intraspecific variations of *M. fuscata* with more individual samples from the northernmost Shimokita Peninsula (located in the northern part of Aomori Prefecture in northernmost Honshu) to the southernmost Yakushima Islands (located in the south of the Kyushu Islands) by the control region sequences, demonstrated that there are major eastern and western lineages in the Japanese Archipelago, and suggested that the eastern lineage experienced the recent northward demographic expansion from a refugium in the post-glacial periods in the Late Quaternary.

Rodentia

Gliridae

There are 28 species in the family Gliridae (Holden 2005), in which almost all the species are observed in Europe and Africa. The Japanese dormouse *Glirulus japonicus* is endemic to Japan and inhabits the HSK region (BP6; Table 3.1). Because *G. japonicus* is the only species within Gliridae that inhabits East Asia, it is extremely difficult to infer the origin of this species in Japan by only investigating the extant species. Nevertheless, Nunome et al. (2007) clarified with three nuclear gene exon sequences (*Apob*, *Irbp*, and *Rag1*) that the closest lineage of *G. japonicus* is the edible dormouse *Glis glis* that is distributed in Europe, and also estimated on the basis of the oldest fossil record of *Glis* (25 MYA) that their divergence occurred 24 to 30 MYA under the background of major glirid diversifications during a relatively warmer climate period from the Early Oligocene (34 MYA) to the Mid-Miocene Climatic Optimum (15–17 MYA). These time estimates suggest that the origin of the Japanese dormouse may have predated the formation of the Japanese Archipelago (about 15 MYA; Neall and Trewick 2008). Additionally, it could be argued that the past 15 million years have seen declines of East Asian dormice because of the climate change into colder and drier environments, which the dormice do not favor (Zachos et al. 2001).

On the other hand, Yasuda et al. (2007, 2012) examined intraspecific variations of *G. japonicus* with mitochondrial *Cytb* and Y-chromosomal *Sry* genes and clarified that *G. japonicus* possesses nine geographic lineages that diversified 3 to 5 MYA. Yasuda et al. (2007) concluded that the divergences into these local populations occurred within the Japanese Archipelago. Furthermore, they showed that the extent of the genetic divergence among the geographically separated populations corresponds to that of interspecific variations in other mammalian groups. Thus, they also suggested that each local population can be regarded as a cryptic species.

Sciuridae

The family Sciuridae is one of the species-rich mammalian groups, including 278 squirrel species distributed across the worldwide continental regions except for Australia and Antarctica (Thorington and Hoffmann 2005). There are three types of ecological lifestyles among squirrels [arboreal (tree squirrels), terrestrial (ground squirrels), and gliding (flying squirrels) locomotors]. Recent molecular phylogenetic analyses of the multiple nuclear and mitochondrial genetic loci have determined five major lineages corresponding to subfamilial level and suggested that the arboreal tree squirrel is the ancestral type that would have had a key role in the major squirrel diversifications and subsequent derivation of the terrestrial and gliding squirrel lineages (Mercer and Roth 2003; Steppan et al. 2004b; Herron et al. 2004). Six squirrels exist in the Japanese Archipelago (Ohdachi et al. 2015), which are assigned to two of these major clades, a clade of arboreal and gliding squirrels (Sciurinae in Steppan et al. 2004b; *Sciurus*, *Pteromys*, and *Petaurista*) and a clade of mostly ground squirrels (Xerinae in Steppan et al. 2004b; *Tamias*). All three locomotor styles can be observed in the squirrels in Japan: the Eurasian red squirrel *Sciurus vulgaris* (arboreal), the Japanese squirrel *Sciurus lis* (arboreal), the Siberian flying squirrel *Pteromys volans* (gliding), the Japanese flying squirrel *Pteromys momonga* (gliding), the Japanese giant flying squirrel *Petaurista leucogenys* (gliding), and the Siberian chipmunk *Tamias sibiricus* (terrestrial, but, in fact, intermediate between terrestrial and arboreal) (Steppan et al. 2004b).

The Japanese sciurid species show clear distributional trends. Namely, congeneric species do not share the same distribution although species in the different genera do coexist in the same region (*S. vulgaris*, *P. volans*, and *T. sibiricus* in Hokkaido and *S. lis*, *P. momonga*, and *P. leucogenys* in the HSK region). Hence, it follows that there are only two biogeographic patterns for the squirrels on the

Japanese Archipelago, BP2 (Table 3.1; *S. vulgaris*, *P. volans*, and *T. sibiricus*) and BP6 (Table 3.1; *S. lis*, *P. momonga*, and *P. leucogenys*). *Sciurus lis* and *P. momonga* in the HSK region has been demonstrated to be each sister lineage to *S. vulgaris* and *P. volans*, respectively (Herron et al. 2004). Because *S. vulgaris* and *P.volans* are also distributed in the Eurasian continent, the Hokkaido lineage of each species would have been generated later than lineages of *S. lis* and *P. momonga*, respectively. It is therefore likely that *S. lis* and *P. momonga* were earlier colonizers in the Japanese islands than *S. vulgaris* and *P. volans*, respectively; this is the same phylogenetic structure observed in the *Sorex* species in the family Soricidae. Although some phylogenetic and phylogeographic studies have been known for *Sciurus* species (Oshida et al. 1996, 2009a; Oshida and Masuda 2000; Grill et al. 2009; Liu et al. 2014), few of these examined time scales for the lineage differentiations or demographic events. Oshida and Masuda (2000) estimated the divergence time between *S. vulgaris* and *S. lis* to be 4.0 to 5.2 MYA based on the 0.5 % transversional substitutions/myr of the *Cytb* gene (Irwin et al. 1991). This value would be an overestimate, probably because of the use of the underestimated substitution rate (from the application of the slowly evolving ungulate rate into the rapidly evolving rodent time scale). Later, Oshida et al. (2005) adopted a 5–10 %/myr divergence rate for the *Cytb* gene considering that the divergence rate was suggested to be variable among rodents within the range of 5–10 %/myr [see Brunhoff et al. (2003) for the rationale]. If I adopt the 5–10 %/myr of divergence rate for the case of *Sciurus* species in Oshida et al. (2000a) where the total difference in *Cytb* between *S. vulgaris* and *S. lis* was inferred to be 4.9–6.8 %, the divergence time between these species is 0.49–1.36 MYA (4.9–6.8 % divided by 5–10 %), which is more consistent with the palaeontological evidence suggesting that the lineage of *S. lis* migrated into Honshu in the Middle Pleistocene period (Kawamura 1988). Although specifying whether the ancestral *S. lis* lineage migrated into the Japanese archipelago via northern or southern routes is not easy, the origin from the Korean Peninsula, the southern route, may be plausible because their absence in Hokkaido can more easily be explained. However, even if it is the case, it is difficult to understand why the ancestral lineage did not reach Hokkaido despite the multiple chances of migration via the land bridges formed in the Tsugaru Strait since the Early to Middle Pleistocene period. Probably, the population expansion might have occurred in the Late Pleistocene as in *Chimarrogale platycephalus*. More extensive phylogeographic and demographic analyses would be needed to grasp the time scale of the population expansion of *S. lis* in the HSK region.

The origin of the Hokkaido lineage of *S. vulgaris* is not clear because there have been no molecular chronological studies comparing the continental and Hokkaido lineages. If I calculate their divergence time on the basis of the *Cytb* sequence data deposited in the DNA database by Oshida and Masuda (2000; Hokkaido, Korean, and Transbaikalian individuals), it was inferred that the Hokkaido lineage diverged from the monophyletic Korean and Transbaikalian lineage 0.18 to 0.36 MYA in the Middle Pleistocene, where the average between genetic distances of the Hokkaido/Korea (1.3 %) and the Hokkaido/Transbaikalia (2.3 %) was divided by the 5–10 %/

myr divergence rate (Oshida et al. 2005). Liu et al. (2014) indicated that there are no geographic structures among populations of *S. vulgaris* from Europe to East Asia and suggested the recent rapid population expansion, although no time frame was provided. My tentative hypothesis is the Middle Pleistocene origin for the Hokkaido lineage of *S. vulgaris*. However, more rigorous phylogeographic studies are needed for future precise time estimations.

For the Eurasian flying squirrel *P. volans*, the Hokkaido population was clarified as a monophyletic lineage (Oshida et al. 2005; Lee et al. 2008), and the divergence from the Eurasian lineages was estimated to have taken place 0.2 to 0.4 MYA based on the 5–10 %/myr divergence rate for the *Cytb* gene (Oshida et al. 2005). For the Japanese flying squirrel *P. momonga*, no studies have been conducted on the intraspecific genetic diversity. Comparison of the *Cytb* gene sequences from the DNA database for both *P. volans* and *P. momonga* (Oshida et al. 2005) enabled me to estimate that the average sequence difference between them was 12.3 %, implying that they diverged 1.2 to 2.5 MYA on the basis of the 5–10 %/myr divergence rate as above (Oshida et al. 2005), which is earlier than the possible origin of the Hokkaido lineage of *P. volans* (0.2–0.4 MYA). As in the case of *S. lis*, the migration route of *S. momonga* is not clear, although the southern route may be more conceivable.

Petaurista constitutes one of the genera encompassing gliding squirrels and is the most closely related to *Pteromys* (Oshida et al. 2000b). In contrast to the genera *Sciurus* and *Pteromys*, species within the genus *Petaurista* are mainly distributed in the southern parts of the Eurasian continent rather than the northern Eurasian regions. Among them, *P. leucogenys*, endemic to Japan, is the most divergent lineage within the genus (Oshida et al. 2000b; Li et al. 2013a, b). Based on the evolutionary rate of Irwin et al. (1991), Oshida et al. (2000a) estimated that the generation of the *P. leucogenys* lineage took place around the Late Miocene period (about 8–10 MYA). Li et al. (2013) also examined the *Cytb* gene and obtained a much older time estimate (12.5 MYA) for the origin of the *P. leucogenys* lineage on the basis of the oldest sciurid fossil record (*Douglassciurus jeffersoni*; 33.9–37.2 MYA) and the earliest fossil of *Petaurista petaurista* (0.6–1.3 MYA) as the calibration points. However, these time values might be results of overestimations: first, because of using the underestimated evolutionary rate of Irwin et al. (1991) as already explained, and second, the time scale of more than 30 MYA for setting the calibration point would be too old for the mitochondrial *Cytb* gene to estimate reliable divergence times because of the severe saturation effect as has been noted. If I apply the 5–10 %/myr divergence rate of *Cytb* to the data of Oshida et al. (2000a), the divergence between *P. leucogenys* and the other congeneric species was estimated to have occurred 1.39 to 3.06 MYA, which is more similar to or slightly more ancient than the date of the origin of similarly the HSK-endemic sciurid species, *S. lis* (0.49–1.36 MYA) and *P. momonga* (1.2–2.5 MYA), and is also more concordant with the palaeontological evidence (the Middle Pleistocene origin) (Kawamura 1988; Kawamura et al. 1989). The phylogeographic analyses of the mitochondrial D-loop region by Oshida et al. (2001) elucidated that there are three divergent lineages in *P. leucogenys* in the Japanese Archipelago and suggested that the Kyushu is the ancestral region for the diversification of this species because the Kyushu population has the most divergent or ancestral haplotypes and two of three major lineages. Combined with the presence of the closely related *Pataurista* species in the southern part of Eurasia, these observations support the southern route immigration hypothesis, which is similar to the situation of *Chimarrogale platycephalus*. The divergence among the three major lineages was estimated to have occurred 0.4 to 1.0 MYA based on the evolutionary rate of the human D-loop sequences (8.6 %/million years; Vigilant et al. 1989). Later, Oshida et al. (2009b) examined the *Cytb* gene and found that there are five distinct phylogroups (Kyushu, Southwest, Southeast, Central, and North), including the three major lineages of Oshida et al. (2001). Using 5–10 %/myr for the divergence rate, they estimated that diversifications among five major lineages occurred 0.09 to 0.24 MYA. These estimates are in agreement with the divergence time between *P. leucogenys* and the closest species (1.39–3.06 MYA). Additionally, Oshida et al. (2009b) detected the trend of the sudden population expansion for only the northern phylogroup that took place 18,200 to 36,500 years ago, suggesting a possibility that the absence of this species in Hokkaido might have been caused by the formation of the Tsugaru Strait in the Late Pleistocene (Ohshima 1991).

Tamias sibiricus is the only Palaearctic species within the genus *Tamias*, in which the other species are all found in the American continent. There have been few phylogeographic studies including the Hokkaido lineage of *T. sibiricus*. Only Obolenskaya et al. (2009) examined one individual from Hokkaido together with many samples from Russia, China, and Korea. They showed that there are at least three divergent lineages in this species, northern Eurasian, Korean, and Central Chinese lineages (but the validity of the last one is still open to question because this is based on pet shop samples with unknown origin). The Japanese chipmunk is included in the northern Eurasian lineage. Although their approach for the divergence time estimation is arbitrary because they forced the divergence among these major lineages to have occurred in the onset of the Middle Pleistocene period without clear explanations for the calibration procedure, the differentiations among lineages within the northern Eurasian clade, including the lineage of Hokkaido, was calculated to have transpired 0.11 to 0.47 MYA in the Middle to Late Pleistocene period. Here again, if I apply the 5–10 %/myr rule to the data of Obolenskaya et al. (2009), the divergence time among the northern Eurasian lineages was estimated to be 0.10 to 0.19 MYA (average genetic difference among 90 individuals within the northern Eurasian clade, 0.95 %, divided by 5–10 %), which is congruent with the estimate of Obolenskaya et al. (2009).

Muridae

The family Muridae is the most speciose family in the order Rodentia and even in the class Mammalia, comprising 150 genera and 730 species (Musser and Carleton 2005). There are six extant species of this family in the Japanese Archipelago, except for the species commensal to our life such as rats (*Rattus* spp.) and house mice (*Mus musculus*) (Ohdachi et al. 2015). These six species are classified into three genera, *Apodemus*, *Micromys*, and *Mus*, all belonging to the subfamily Murinae. The Murinae is the most diversified subfamily within the Muridae, and the interrelationships among the major lineages (genera) within this subfamily have remained to be elucidated because of the rapid diversifications during a relatively short evolutionary time span (Sato and Suzuki 2004; Steppan et al. 2005).

Species in the genus *Apodemus* are mainly adapted to the deciduous broad-leaved forest in northern Eurasia across Europe to East Asia, including the Japanese Archipelago (Musser and Carleton 2005). Molecular phylogenetic studies have clarified that there are four major lineages among 20 species in *Apodemus* (Serizawa et al. 2000; Suzuki et al. 2003, 2008): the *argenteus* lineage endemic to Japan, the *gurkha* lineage endemic to Nepal, the lineage mainly occupying the East Asia, and the lineage mainly observed in Europe. Four species are found in Japan, the striped field mouse *A. agrarius*, the small Japanese field mouse *A. argenteus*, the East Asian field mouse *A. peninsulae*, and the large Japanese field mouse *A. speciosus*, showing three biogeographic patterns (BP2, BP5, and BP10, respectively; Table 3.1). Based on the nuclear gene variations (*I7*, *Irbp*, *Rag1*, and *vwf*), Suzuki et al. (2008) estimated that lineages of *A. argenteus* and *A. speciosus* occurred 7.3 and 5.9 MYA, respectively, based on the *Mus*–*Rattus* divergence at 12 MYA. Because more closely related species are missing in continental Asia, it is supposed that the formation of the Japanese Archipelago might have affected the generation of such highly divergent endemic species. Because the time estimates for the generation of *A. argenteus* (7.3 MYA) and *A. speciosus* (5.9 MYA) correspond to the Late Miocene age that saw the vegetation changes promoted by the environmental shift to a colder and drier climate (Cerling et al. 1997), some researchers supposed that these climate changes might have facilitated the diversification of the *Apodemus* lineages (Serizawa et al. 2000; Michaux et al. 2002; Suzuki et al. 2003, 2008). Regarding the intraspecific phylogeographic studies, Suzuki et al. (2004) examined the mitochondrial *Cytb* gene for *A. speciosus* and *A. argenteus* from all the major islands and neighboring small islands, and estimated, with the evolutionary rate of 2.4 %/lineage/myr (Suzuki et al. 2003), that the most basal divergence in *A. speciosus* and *A. argenteus* occurred 0.51 and 0.64 MYA, respectively. Notably, they detected two major clades in *A. speciosus* separating central (Honshu, Shikoku, and Kyushu Islands) and peripheral (Hokkaido, Sado, Izu, and Satsunan Islands) lineages. Tomozawa and Suzuki (2008) basically obtained supportive evidence from the nuclear gene (*Irbp*) for the central/peripheral trend, although the Hokkaido and Sado lineages were included in the central lineage, the Satsunan lineages were observed in both lineages, and the Oki and Tsushima lineages were added to the peripheral lineage. Tomozawa and Suzuki (2008) discussed that allopatric fragmentation might have caused the generation of the central and peripheral lineages, and the recent population expansion at 0.14 MYA (based on 2.4 %/lineage/myr as earlier) formed the current distribution pattern of the central lineage, where the male-biased dispersal might replace the nuclear genome of Hokkaido, Sado, and a part of Satsunan populations with the peripheral mtDNA types that remained because of female philopatry. It should be noted here that although all the dating estimates are fundamentally based on the frequently used divergence time between *Mus* and *Rattus* (12 MYA), the recent palaeontological (11.0–12.3 MYA; Benton and Donoghue 2007) and molecular phylogenetic (8.6–10.3 MYA; Steppan et al. 2004a) studies have gradually supported younger dates than 12 MYA. Therefore, the real divergence and population expansion times could also be more recent than obtained here based on the 12 MYA for the *Mus–Rattus* divergence.

Serizawa et al. (2002) conducted phylogeographic research with the mitochondrial *Cytb* gene for *A. peninsulae* and clarified the monophyly of the Hokkaido population to the continental one. The estimate for the divergence time of the Hokkaido lineage from the continental equivalent in the most recent study was 0.1 MYA in the Late Pleistocene, based on fossil calibrations that the divergence between *A. mystacinus* and the other *Sylvaemus* species and that between *A. sylvaticus* and *A. flavicollis* occurred 7 and 4 MYA, respectively (Sakka et al. 2010; also based on *Cytb*). This dating is consistent with the absence of this species in the other southern Japanese islands because of the presence of the Tsugaru Strait in the Late Pleistocene as in the case of *Sorex minutissimus* and *Sorex gracillimus* (Ohshima 1991). Both these studies indicated that the population from Siberia to the Russian Far East harbors a higher extent of genetic diversity, therefore implying the existence of refugia in the glacial periods in the Pleistocene. Probably the Hokkaido lineage is a result of the population expansion from the refugial region in Far East Asia (Serizawa et al. 2002; Sakka et al. 2010).

The harvest mouse *Micromys minutus* has a wide distribution from Europe to the easternmost islands of Japan (BP7; Table 3.1) and mainly favors open environments (e.g., grasslands; Ohdachi et al. 2015). Interestingly, the intraspecific genetic variation was inferred to be very small according to the phylogeographic research based on the mitochondrial *Cytb* gene and control region sequences (Yasuda et al. 2005), which is suggestive of the recent rapid population expansion across wide areas in Eurasia. Yasuda et al. (2005) estimated on the basis of 2.4 %/lineage/myr (Suzuki et al. 2003) that the divergence between the Japan/Korea and European lineages occurred 0.08 MYA in the Late Pleistocene and also suggested that the population expansion within the Japanese Archipelago occurred 0.03 MYA. Such a recent establishment of this species in Japan is in agreement with the lack of any fossil records of this species in Japan (Ohdachi et al. 2015). On the other hand, such estimates for the Late Pleistocene origin of *M. minutus* in Japan would not agree with the argument of Ohshima (1991) that the Korea (Tsushima) Strait was not available by land bridges in this age. I discussed the possible process of the origin of *M. minutus* in the text (oversea dispersal hypothesis). Here again, also note that dating with the 2.4 %/lineage/myr rate of Suzuki et al. (2003) based on the 12 MYA for *Mus–Rattus* divergence is likely to lead to overestimations of divergence and expansion times.

It has been repeatedly debated, and still remained to be resolved, whether the establishment process of the Ryukyu mouse *Mus caroli* in the Ryukyu Islands (BP10; Table 3.1) was natural or human induced (Motokawa 2000; Motokawa et al. 2003). Terashima et al. (2003) showed that *M. caroli* possesses a unique mitochondrial *Cytb* gene lineage that is not found in the other populations in Southeast Asia and concluded that it was established by a natural dispersal instead of an anthropogenic effect. On the other hand, Shimada et al. (2007) used the same genetic loci for individuals from much wider sampling localities and presented the opposite conclusion for human commensalism in the prehistoric age in Japan, because the *M. caroli* in Ryukyu Islands was shown to be closely related to the Laos lineage within a strongly supported clade of the southern Southeast Asian clade and did not show close affinity with the geographically close Taiwan lineage. Because of this ambiguous status, I did not consider this species in discussions.

The remaining Murinae species are included in the Ryukyu-endemic genera *Tokudaia* and *Diplothrix*. Three *Tokudaia* species, the Okinawa spiny rat *T. muenninki*, the Amami spiny rat *T. osimensis*, and the Tokunoshima spiny rat *T. tokunoshimensis*, are each distributed in Okinawajima, Amami-Oshima, and Tokunoshima Islands, respectively, in the Ryukyu region [BP9; Table 3.1; also see Endo and Tsuchiya (2006) and Ohdachi et al. (2015)]. Molecular phylogenetic studies have demonstrated that *Tokudaia* formed a clade with *Apodemus* (Michaux et al. 2002; Sato and Suzuki 2004), and the divergence time between these species was estimated to be 6.5–8.1 MYA by nuclear gene analyses (*Irbp* and *Rag1*; Sato and Suzuki 2004). To date, few studies have examined the chronology for interspecific divergence within *Tokudaia*. Suzuki et al. (1999) suggested with rDNA-RFLP data that the lineages in Amami–Oshima and Tokunoshima diverged 1.2 to 2.3 MYA based on the previously estimated evolutionary rate of 1–2 %/myr, whereas the time was 4.4 MYA based on a partial *Cytb* gene data although it depended on the evolutionary rate of Brown et al. (1979). Murata et al. (2010) demonstrated that *T. muenninki* was first branched off in the phylogeny among three *Tokudaia* species, meaning that two Y-chromosome-lacking *Tokudaia* species, *T. osimensis* and *T. tokunoshimensis*, formed a clade. According to the *Cytb* gene sequences provided by Murata et al. (2010), average pairwise difference between *T. muenninki* and the other two species was 12.4 % and that beween *T. osimensis* and *T. tokunoshimensis* was 5.4 %, which could be calculated to be 2.58 and 1.13 MYA, respectively, on the basis of the 2.4 %/lineage/myr substitution rate (Suzuki et al. 2003).

The Ryukyu long-furred rat *Diplothrix legata* is a monotypic species inhabiting the Amami–Oshima, Tokunoshima, and Okinawajima Islands in the Ryukyu region (BP9; Table 3.1; also see Ohdachi et al. 2015). Suzuki et al. (2000) examined the nuclear *Irbp* and the mitochondrial *Cytb* genes and supported that *Diplothrix legata* is closely related to a clade consisting of *Rattus rattus* and *Rattus argentiventer* to the exclusion of *Rattus norvegicus*, strongly implying the paraphyly of the genus *Rattus* to *Diplothrix*. They also showed that the extent of the divergence between *Diplothrix* and *Rattus* species corresponds to 20–30 % of that between *Mus* and *Rattus*. Although Suzuki et al. (2000) estimated the divergence time to be 3–4 MYA, it was based on 14 MYA for the *Mus–Rattus* split, which is not consistent with the current knowledge as already noted (8.6–10.3 MYA, Steppan et al. 2004a; 11.0–12.3 MYA, Benton and Donoghue 2007). If I adopt the average 10.55 MYA {([8.6 + 10.3]/2 + [11 + 12.3]/2)/2}, 20–30 % means 2.11–3.17 MYA for the divergence of the lineage for *D. legata*. This time estimate is consistent with the geological evidence in Kimura (2000) that the Ryukyu Islands were connected multiple times to the Eurasian continent in two stages, the former of which was 1.3 to 1.6 MYA.

Cricetidae

The family Cricetidae is the second most speciose family in the order Rodentia, comprising 130 genera and 681 species (Musser and Carleton 2005). Except for the introduced species (the muskrat *Ondatra zibethicus*), there are six cricetid species in the Japanese archipelago, all of which are classified in the subfamily Arvicolinae (Kaneko 2006; Ohdachi et al. 2015). Although confusion has surrounded the taxonomy within this subfamily, in this chapter I followed Musser and Carleton (2005) and Carleton et al. (2014) for the genus name, but basically adopted the common names and species numbers in Ohdachi et al. (2015). Thus, the Japanese cricetid species discussed in this chapter are the northern red-backed vole *Myodes rutilus*, the grey red-backed vole *Myodes rufocanus*, the dark red-backed vole *Myodes rex*, the Anderson's red-backed vole *Myodes andersoni*, the Smith's red-backed vole *Myodes smithii*, and the Japanese field vole *Microtus montebelli*.

The five *Myodes* species are adapted to the forested environments in the Hokkaido and HSK regions. *M. rutilus*, *M. rufocanus*, and *M. rex* similarly have their native ranges in Hokkaido, but show different distribution patterns outside Hokkaido, expanding to Holarctic (BP1), Palaearctic (BP2), and Sakhalin (BP3) regions, respectively (Table 3.1). The origins of these three species in Hokkaido are considered independent of each other. Kohli et al. (2015) conducted extensive phylogeographic analyses for *M. rutilus* across Eurasian and American continents by using the mitochondrial *Cytb* and three nuclear genes (*Ets2*, *Irbp*, and *Mlr*). They found that there are distinct phylogroups that would have been derived from at least three refugia located in western Eurasia, central Eurasia, and Beringia. The divergences among these phylogroups were estimated to have occurred during the last 0.1 million years in the Late Pleistocene. It was also suggested that the monophyletic Hokkaido lineage was possibly originated by the expansion from a northern refugium, Beringia. If the establishment of this species in Hokkaido originally occurred in the Late Pleistocene, it can explain the absence of this species in more southern Japanese islands because of the same reason for *Sorex minutissimus*, *S. gracillimus*, and *Apodemus peninsulae* (the hypothesis of the Tsugaru Strait barrier in the Late Pleistocene; Ohshima 1991). On the other hand, for *M. rufocanus*, Abramson et al. (2012) estimated with the *Cytb* gene and the palaeontological information (the differentiation among European haplotypes occurred 8,000 years ago; the divergence between *M. rutilus* and *M. glareorus* at 2.5 MYA) that the monophyletic Hokkaido lineage diverged from the clade mainly composed of the Far East Russian and Sakhalin lineages 0.27 MYA and experienced the population expansion 0.04–0.05 MYA in Hokkaido. Although Abramson et al. (2012) did not provide intra-lineage dating information, the most recent common ancestor of the Hokkaido individuals could be estimated to be present in the Late Pleistocene (<0.13 MYA), inferred from the branch length of the phylogeny that they provided. Therefore, the absence of *M. rufocanus* in Honshu and the more southern islands may be explained by the Tsugaru Strait barrier in the Late Pleistocene as in the case of *M. rutilus*. Abramson et al. (2012) further suggested that there should have been multiple refugia in the Russian Far East because the population possesses higher genetic diversity there, implying that the Hokkaido lineage originated from the expansion from the refugia in the Russian Far East, which is in sharp contrast to the original source for the population expansion of *M. rutilus* (Beringia), but consistent with the case of *Apodemus peninsulae* in the light of space (not time). *M. rex* can be regarded as the earliest colonizer among three *Myodes* species in Hokkaido because the divergence from the most closely related lineage (*M. rufocanus*) was estimated to have occurred in the Middle Pleistocene (0.81 MYA; Abramson et al. 2012). Based on the results of the mitochondrial DNA control region, Kawai et al. (2013) detected four phylogroups from the several fragmented populations in Hokkaido and concluded that such phylogroups were shaped by the genetic divergences across several refugia formed in the glacial periods since the Middle Pleistocene. This conclusion is because in their study the time to the MRCA of the *M. rex* phylogroups was estimated to be 0.12–0.58 MYA in the Middle Pleistocene based on the "mutation" rate of 3.6 %/myr (based on the divergence time of 7–8 MYA between *Microtus* and *Clethrionomys* (in this case *M. rutilus*, *M. rufocanus*, and *M. rex* are all included in this genus) (Matson and Baker 2001) and 17 %/myr (based on the divergence time of 1.8 MYA for the Siberian and the Nearctic brown lemmings; Fedorov and Stenseth 2001) estimated for the arvicoline control region diversity. However, despite that these rates were originally proposed as "divergence" rates considering two descendant lineages, Kawai et al. (2013) adopted them as per-lineage mutation rates. Therefore, the foregoing estimates (0.12–0.58 MYA) should be corrected to 0.24–1.16 MYA. The corrected estimates also largely include the Middle Pleistocene period and are not inconsistent with the divergence of the *M. rex* lineage as estimated above (0.81 MYA). It is not clear why *M. rex* did not reach more southern Japanese islands despite the presence of the land bridge in the Tsugaru Strait in the Middle Pleistocene, but a community ecological mechanism may explain the absence in Honshu and more southern islands.

Two *Myodes* species in the HSK region, *M. andersoni* and *M. smithii*, are endemic species in Japan (BP6; Table 3.1). The former was mainly found in the eastern Honshu and the latter in the western Honshu, Shikoku, and Kyushu, while their distributions are partly overlapped in the central Honshu. Their ancestral common lineage was inferred to have diverged 0.9 to 2.3 MYA from the clade composed of *M. rufocanus* and *M. rex* (Luo et al. 2004; Lebedev et al. 2007; Kohli et al. 2014). Although the time estimates are variable among studies, it is probable that the *Myodes* species in the HSK region might have originated in the Early to Middle Pleistocene, much earlier than that of the *Myodes* species in Hokkaido. However, the patterns of lineage differentiations within and between *M. andersoni* and *M. smithii* are quite complicated. *M. simthii* is not monophyletic in the phylogeny inferred by the *Cytb* gene. Namely, the lineage in Shikoku was shown to be the most divergent among all the lineages detected in *M. andersoni* and *M. smithii*, and the *M. smithii* lineage composed of haplotypes detected in Honshu and Kyushu was closely related to *M. andersoni* (Iwasa and Suzuki 2002). Time scales for the differentiations have not been fully assessed to date in a reliable manner. Assuming that the time to the MRCA of the red-backed voles was 1.8 MYA, Luo et al. (2004) suggested that the Shikoku lineage of *M. smithii* diverged from the rest 0.77 MYA, and the Honshu–Kyushu lineage of *M. smithii* diverged from *M. andersoni* 0.16 MYA. Kohli et al. (2014) estimated with the fossil calibration (2.6 MYA for the time to the MRCA of *Myodes* species based on the oldest fossil found in Russia) that *M. smithii* in Honshu diverged from *M. andersoni* 0.50 MYA. These time estimates might be too recent to be regarded as those for valid species differentiation. Iwasa and Suzuki (2003) detected “interspecific” hybridization between both species. Kaneko (2006) mentioned that it is difficult to identify the *Myodes* species in Honshu by morphological criteria only. Probably future taxonomic revision would be needed on the basis of more rigorous morphological and molecular phylogenetic studies for the *Myodes* species in the HSK region. Alternatively, it is also probable that the ancestral polymorphisms of both species have been retained since the divergence between *M. andersoni* and *M. smithii*. Female philopatry might have influenced the maintenance of such divergent lineage in the mitochondrial gene. Iwasa and Suzuki (2002) suggested that both Honshu and Shikoku populations have the same type of Y-chromosomal *Sry* gene, which is male specific and irrelevant for the female philopatry. Also in this case, all the populations may be assigned to one *Myodes* species.

Microtus is the most speciose genus within the subfamily Arvicolinae (62 species; Musser and Carleton 2005) and includes mainly herbivorous small rodents adapted to grasslands, taiga, steppe, and tundra. There is only one *Microtus* species in Japan, *M. montebelli*, which is endemic to and distributed in Honshu and Kyushu regions (BP6; Table 3.1). It is phylogenetically closely related to *M. oeconomus*, widely distributed in Holarctic regions in the Eurasian and American continents, and *M. kikuchii*, endemic to the Taiwan Islands (Conroy and Cook 2000; Jaarola et al. 2004; Bannikova et al. 2010). There have been few studies that examined chronological aspects of this species based on molecular data. Bannikova et al. (2010) only estimated with the mitochondrial *Cytb* gene and the time constraint of 2.2 MYA for the radiation of the basal *Microtus* lineages (based on fossils) that *M. montebelli* diverged from the aforementioned closely related species 0.95 MYA. The time estimate is similar to that of the *Myodes* species in HSK. In the fossil evidence, this species was found since the Middle Pleistocene (Kawamura et al. 1989). The estimated time scale suggests that there should have been some possibilities that *M. montebelli* could have expanded to all the Japanese islands, Hokkaido, Honshu, Shikoku, and Kyushu. The absence of this species from Hokkaido and Shikoku requires some explanation in light of phylogeography or ecology. Kaneko (2006) discussed that the interspecific competition with *Apodemus* species might be one reason for the absence of *M. montebelli* in Shikoku. Future studies in the phylogeography and comparisons of niche requirements between

M. montebelli and species in the same guild would shed more light on the reasons for the peculiar distribution pattern of this species.

Lagomorpha

Leporidae

Leporidae is the most species-rich lagomorph family, encompassing 61 species belonging to 11 genera (Hoffmann and Smith 2005). In Japan, 3 species are present and their distributions are geographically partitioned. The mountain hare *Lepus timidus* is distributed in Hokkaido and expanded to the Palaearctic region in the Eurasian continent (BP2; Table 3.1), the Japanese hare *Lepus brachyurus* is endemic to Japan and only observed in the HSK region (BP6; Table 3.1), and the Amami rabbit *Pentalagus furnessi* exists only in Amami–Oshima and Tokunoshima Islands in the Ryukyu region (BP9; Table 3.1). Considering the difference in the extent of endemism in most Japanese mammals among these three major biogeographic regions, it could be predicted that *P. furnessi*, *L. brachyurus*, and *L. timidus* migrated into the Japanese Archipelago in this order. Matthee et al. (2004) conducted molecular phylogenetic analyses with two mitochondrial (*Cytb* and *12S rRNA*) and five nuclear (*Sptbn1*, *Prkci*, *Thy*, *Tg*, and *Mgf*) genes and showed that the genus *Pentalagus* is closely related to the genera *Caprolagus* in India, *Oryctolagus* in Europe, and *Bunolagus* in South Africa, and the divergence of *Pentalagus* from the other genera was 9.44 MYA in the total data analysis and 8.63 MYA in the nuclear gene data analysis on the basis of the palaeontological records (Leporidae–Ochotonidae split, 20–40 MYA; the origin of the modern leporid, 12–20 MYA; the divergence of the genus *Lepus*, 4–6 MYA; the oldest divergence time of the ingroup, 60 MYA). Probably the former value (9.44 MYA) would be overestimated because the mitochondrial genes were included in the examined data matrix. The latter estimate (8.63 MYA) is not contradicted by the Late Miocene origin of the murine rodent genus *Tokudaia*, also endemic to the Ryukyu region (6.5–8.0 MYA; Sato and Suzuki 2004; also see above). Yamada et al. (2002) indicated by using the mitochondrial *12S rRNA* and *Cytb* genes that the mountain hare (*Lepus timidus*) in Hokkaido has a distinct monophyletic lineage and is closely related to *L. arcticus*, *L. townsendii*, and *L. othus* in Greenland and North America, forming a well-supported clade [*L. timidus* group; *L. arcticus*, *L. townsendii*, and *L. othus* are suspected to be the same species as *L. timidus* (Wu et al. 2005)]. In Yamada et al. (2002), *L. brachyurus* was sister to the *L. timidus* group (albeit with a low support value), whereas the position of *Pentalagus furnessi* was not resolved on the earlier radiation among different leporid genera. Assuming the molecular clock of the *Cytb* gene evolution and setting 30 to 40 MYA for the divergence between Ochotonidae and Leporidae, the times for the divergence of *P. furnessi*, *L. brachyurus*, and the Hokkaido lineage of *L. timidus* from each sister lineage were estimated to be 12–16 MYA, 4–5 MYA, and 0.5–0.6 MYA, respectively (Yamada et al. 2002). In addition, Wu et al. (2005) examined four mitochondrial genetic loci (*Cytb*, *Nd2*, *12S rRNA*, and *Dloop*) for the extensive *Lepus* species, and indicated that the *L. brachyurus* first branched off in the clade composed of Eurasian *Lepus* species. Wu et al. (2005) also estimated with the *Cytb* gene that the divergence time for the branching of the *L. brachyurus* lineage was 3.62 MYA, which is not in disagreement with the estimate within the Pliocene in Yamada et al. (2002). However, the estimate of Yamada et al. (2002) for the origin of *Pentalagus* (12–16 MYA) is much earlier than that of Matthee et al. (2004) (8.63 MYA), which mainly used nuclear genes. The difference would be attributed to the distinct properties between mitochondrial and nuclear genes for dating divergences, as repeatedly discussed earlier. Therefore, the divergence times of Yamada et al. (2002) and Wu et al. (2005) might be somewhat overestimated because of the exclusive use of the mitochondrial genes. If I conduct a simple calculation that 8.63 MYA is 62 % of 14 MYA (average between 12 and 16 MYAs) and apply this proportion to the other estimates of Yamada et al. (2002), 4–5 MYA for *L. brachyurus* and 0.5–0.6 MYA for *L. timidus* are calculated to be 2.48–3.10 MYA and 0.31–0.37 MYA, respectively.

On the basis of the phylogeographic analyses of the intraspecific variation in the *Cytb* gene for *L. brachyurus*, Nunome et al. (2010) detected major two lineages (northern and southern lineages) and suggested several regions for refugia during the Pleistocene glacial periods (Kanto, Chubu, Shikoku, and Kyushu), where the genetic diversity was estimated to be higher. These two major clades were inferred to have diverged 1.2 MYA following the lineage-specific evolutionary rate of 1.4 %/lineage/myr (therefore, 2.8 % divergence rate) on the basis of the assumption that *L. timidus* and *L. brachyurus* diverged 3.6 MYA (Wu et al. 2005). Their recent study on the nuclear male-specific *Sry* gene also indicated a similar but a little younger divergence time between northern and southern lineages (1.07 MYA; Nunome et al. 2014). Nunome et al. (2010) also showed that the initial divergence in each northern and southern clade occurred 0.33 MYA and 0.38 MYA, respectively. The ages raised here are in agreement with the palaeontological record that the fossil remains were found in Japan in the Middle Pleistocene (Kawamura et al. 1989). Additionally, the multiple locations for refugia suggested by Nunome et al. (2010) are consistent with those of the water shrew (Iwasa and Abe 2006), macaque (Kawamoto et al. 2007), and Japanese giant flying squirrel (Oshida et al. 2009b).

In the phylogeographic analyses with the *Cytb* gene, Kinoshita et al. (2012) elucidated that the Hokkaido lineage of *L. timidus* diverged from the most closely related Korean lineage, *L. coreanus*, 0.30 MYA and that the ancestral lineage including both *L. timidus* in Hokkaido and *L. coreanus* was separated from the other Eurasian *L. timidus* lineages 0.46 MYA. The adopted assumptions for calibration points were the divergence between *Oryctolagus* and *Lepus*, 11.8 MYA; the time to the MRCA of *Lepus*, 5.16 MYA; the divergence between *L. timidus* and *L. townsendii*, 1.13 MYA. The estimates obtained by Kinoshita et al. (2012) are consistent with the already calculated divergence time of the Hokkaido lineage of *L. timidus* (0.31–0.37 MYA). Because the Sakhalin lineage was demonstrated to be included in the Eurasian clade, the colonization of the eastern marginal islands off the Eurasian continent by the lineage of *L. timidus* would have occurred more than twice, in which one could reach Hokkaido but the other stopped at Sakhalin. The time to the MRCA of Hokkaido lineages was estimated to be 0.17 MYA in this study, suggesting that the origin of the *L. timidus* population in Hokkaido was in the Middle Pleistocene, although an extent of overestimation might be suspected because of the use of the mitochondrial gene and little old fossil assumption. Furthermore, they clarified that there were two distinct lineages in Hokkaido that would have been created through within-island vicariance into two southern refugia in Hokkaido.

To sum the foregoing discussions, despite the presence of some uncertainties in the chronological estimates for three leporid species in Japan, all the estimations here are consistent with the prediction that *P. furnessi*, *L. brachyurus*, and *L. timidus* colonized the Japanese Archipelago in this order.

Ochotonidae

The family Ochotonidae includes only one genus, *Ochotona*, composed of 30 pika species (Hoffmann and Smith 2005). Among the 28 *Ochotona* species distributed in Asia, only 1 species, the northern pika *Ochotona hyperborea*, exists in Hokkaido among the Japanese Archipelago, and this species is also distributed in the Palaearctic region in Eurasia (BP2; Table 3.1). Previous molecular phylogenetic analyses have indicated that the lineage of *O. hyperborea* itself is closely related to *O. scorodumovi* inhabiting continental East Asia, and the Hokkaido lineage of *O. hyperborea* is the most genetically distinct among the other Eurasian conspecific lineages (Lissovsky et al. 2007; Lanier and Olson 2009). The estimation of the divergence time with the *Cytb* gene conducted by Niu et al. (2004) implied that most among-species divergence within the genus *Ochotona* occurred in the Early Pleistocene on the basis of the divergence rate of what is stated as 2–5 %/myr of Irwin et al. (1991), although such a rate was not proposed in that study. The lineage of *O. hyperborea* was also estimated to have occurred in this period. In contrast, Lanier and Olson (2009) similarly estimated with the mitochondrial *Cytb* and *Nd4* gene that *O. hyperborea* diverged from *O. scorodumovi* in the Late Pliocene based on the divergence time of 37 MYA for the split between Ochotonidae and Leporidae, but did not provide any information about the time scale for the origin of *O. hyperborea* in Hokkaido despite examining the sample from Hokkaido in their analyses. It is suspicious that these two dating trials did not grasp the realistic time scale because of using the divergence rate of Irwin et al. (1991) and a too-old calibration point (37 MYA) for the *Cytb* gene. In addition, Yu et al. (2004) used the 10 % silent divergence rate/myr of Irwin et al. (1991; this rate was noted in this study) and different time constraints. However, as repeatedly described here, the evolutionary rate extracted from the ungulate taxa is difficult to apply to other taxa because of the difference in the evolutionary rate among mammalian taxa. Lissovsky et al. (2007) showed that the pairwise distance of the *Cytb* gene between the Hokkaido and the continental lineages is 4.53 %. If I adopt the 2.8 %/myr divergence rate used for *Lepus brachyurus* (Nunome et al. 2010), the lineage of *O. hyperborea* in Hokkaido could be interpreted to have occurred 1.62 MYA, which is unusually old for the common species inhabiting only Hokkaido in Japan.

Carnivora

Felidae

Felidae is the second largest family in the order Carnivora, including 40 species (Wozencraft 2005). In contrast to the species-rich trend of this group, only 1 extant species is present in Japan, the leopard cat *Prionailurus bengalensis*. This species is widely distributed in South, Southeast, and East Asia (Wozencraft 2005), whereas in Japan it can only be observed in two isolated islands, Tsushima and Iriomotejima Islands (BP10; Table 3.1) (also see Ohdachi et al. 2015). They are designated as two different subspecies, *P. b. euptilurus* and *P. b. iriomotensis*, respectively (Ohdachi et al. 2015). Although traditionally these two subspecies were sometimes treated as different species or genus, molecular phylogenetic studies have demonstrated that they are phylogenetically so close to the continental conspecific lineages to the extent of the intraspecific variation (Masuda et al. 1994; Masuda and Yoshida 1995; Tamada et al. 2008). The phylogenetically closest species was inferred to be the fishing cat *P. viverrinus*, mainly inhabiting Southeast Asia, and the divergence time was estimated to be 2.55 MYA based on the nuclear and mitochondrial gene segments (~23 kb) with many fossil calibration points (Johnson et al. 2006; also see their Supporting Online Material for the calibration points). Tamada et al. (2008) conducted a phylogeographic study of the Asian leopard cats by using the two mitochondrial genetic loci (*Cytb* and control region) and showed that there are three major lineages (one northern lineage and two southern lineages), where two Japanese leopard cats were included in the northern lineage. Assuming the substitution rate of the *Cytb* gene to be 1.38 %/lineage/myr (2.76 %/myr divergence rate) based on the divergence time of 4.5 MYA between the domestic cat and the tiger (Masuda et al. 1994), the Tsushima leopard cat was estimated to have diverged 0.03 MYA from the continental Far East individual. However, the calibration point in Masuda et al. (1994) is not consistent with recent understandings for the divergence between the domestic cat and the tiger. If I adopt the information from Johnson et al. (2006) where divergence time between them was estimated to be 10.8 MYA (more than twice as much as 4.5 MYA), the divergence time (0.03 MYA) of the Tsushima leopard cat was corrected to be 0.072 MYA by using the 1.15 %/myr divergence rate [=2.76 divided by 2.4 (=10.8/4.5)]. It is not clear how the Tsushima leopard cat migrated into Tsushima Islands and not into the Kyushu Islands in the situation that the water depth is deeper in the sea between Tsushima and the continent than that between Tsushima and Kyushu (Park et al. 2000). Some ecological or environmental reasons should have caused the absence in the main islands in Japan (see Sect. 3.4.2 in the text). Although Tamada et al. (2008) did not infer the divergence time of the Iriomote leopard cat, the average genetic distance between the Iriomote leopard cat and the closest lineage (0.3 %) can be interpreted to be 0.264 MYA based on the corrected fossil assumption. This time estimate is not inconsistent with geological evidence of Kimura (2000) that the Ryukyu Islands were connected twice to the Eurasian continent; the latter connection occurred 0.2 to 0.025 MYA. Therefore, the geological factor could have affected the establishment of the Iriomote leopard cat.

Canidae

Canidae currently includes 35 dog-related species among 13 genera (Wozencraft 2005). Except for the extinct grey wolf *Canis lupus*, there are only 2 species in Japan, the red fox *Vulpes vulpes* and the raccoon dog *Nyctereutes procyonoides* (Ohdachi et al. 2015). They are both distributed across the major Japanese islands (Hokkaido, Honshu, Shikoku, and Kyushu) and the same species are also present in the Eurasian and American continents (therefore, BP = 4; Table 3.1). Although there have relatively been few studies on the molecular phylogeny of this family as a whole, Lindblad-Toh et al. (2005) conducted molecular phylogenetic analyses with nuclear gene sequences of approximately 15 kb and found that both species were placed in one of four major clades in Canidae (the red fox-like clade), where *V. vulpes* formed a clade with the Ruppell’s fox, *Vulpes ruppellii*, distributed from West Asia to Northern Africa, whereas *N. procyonoides* was closely related to the bat-eared fox *Otocyon megalotis* living in Africa. Bardeleben et al. (2005) also obtained consistent results on the basis of molecular phylogenetic analyses with data from 6 nuclear and 2 mitochondrial genes. Perini et al. (2010) examined 3 mitochondrial and 22 nuclear genes and estimated on the basis of the fossil-based minimum bound of 40 MYA for the divergence between Canidae and Ursidae, 7.5 MYA for the divergence between *Ailuropoda* and *Ursus* (this constraint were based on the oldest fossil of *Ailurarctos* at 7–8 MYA, but may have to be corrected as a consequence of the recent report that the oldest remain of the giant panda lineage was found at 11–12 MYA; Abella et al. 2012), and 8 MYA for the divergence between Canini and Vulpini that the time for occurrence of the *N. procyonoides* lineage was 7.7 MYA. Unfortunately, to date, no time frame has been proposed for the divergence between *V. vulpes* and *V. ruppellii*. Only Perini et al. (2010) inferred that the divergence between *V. vulpes* and the Corsac fox *V. corsac*, the closest relative of the *V. vulpes*–*V. ruppellii* clade, was about 2.0 MYA.

Concerning intraspecific phylogeographic studies, Inoue et al. (2007) detected two major mitochondrial DNA (*Cytb*) lineages of *V. vulpes* in Japan, where one is observed in both Honshu/Kyushu and Hokkaido (lineage I) and the other exclusively in Hokkaido (lineage II or Hokkaido II). Precise inspection with longer mitochondrial DNA sequences (*Cytb*, control region, and some *tRNA* sequences) revealed that the lineage I included two distinct clades of the Hokkaido individuals

(Hokkaido Ia and Ib) and a Honshu/Kyushu-specific clade, suggesting that the establishment of *V. vulpes* in the HSK region took place by only one event, whereas multiple migrations might have generated the lineages in Hokkaido (Inoue et al. 2007). A recent phylogeographic study with more extensive samples from western Europe through East Asia including Japan to North America clarified that all the four major lineages observed in Japan (Hokkaido Ia, Ib, II, and Honshu/Kyushu) each have closest relatives in the Eurasian continent, confirming the multiple independent migrations into the Japanese Archipelago (Kutschera et al. 2013). Based on the variations in the mitochondrial control region with external and tip calibrations from fossil and ancient DNA data, respectively, Kutschera et al. (2013) estimated that the divergences of Honshu/Kyushu and Hokkaido II lineages from each continental relative occurred 0.021–0.064 MYA and 0.027–0.045 MYA, respectively, suggesting Late Pleistocene origins. In the same study, Hokkaido Ia and Ib lineages were inferred to have occurred during a more recent part of the Late Pleistocene, probably after the Last Glacial Maximum. However, these time estimates are not concordant with the fossil evidence that the fossil remains of *V. vulpes* were found in the HSK region in the Middle Pleistocene (Kawamura et al. 1989). Because Tsugaru and Korea (Tsushima) Straits were basically not available for dispersals in the Late Pleistocene period, as repeatedly noted (Ohshima 1991), the establishment of the Honshu–Kyushu lineage would have occurred in the Middle Pleistocene. This idea is in sharp contrast to the conclusion of Kutschera et al. (2013) that the Honshu–Kyushu lineage is a consequence of human introduction in the Late Pleistocene. One reason for these younger estimates of Kutschera et al. (2013) may be reflected in too much higher substitution rates obtained by their analyses (33.2–41.9 %/lineage/myr). If I adopt the 1.90–2.68 %/myr divergence rate of the control region obtained from the study of the Japanese weasel *Mustela itatsi* (Masuda et al. 2012; see the following Mustelidae section) and conduct a simple proportion calculation from the 33.2–41.9 %/lineage/myr substitution rate, the divergences times of Honshu–Kyushu and Hokkaido II (estimated earlier to be 0.021–0.064 MYA and 0.027–0.045 MYA) were corrected to 0.52–2.88 and 0.66–1.98 MYA, respectively. The age around the Last Glacial Maximum (~0.02 MYA) estimated for the origin of the Hokkaido Ia and Ib can be calculated to be 0.50–0.88 MYA.

One of the few phylogeographic studies treating the Japanese lineages of *N. procyonoides* is that by Kim et al. (2013), who examined the *Cytb* gene for individuals mainly from Far Eastern Asia including the Japanese Archipelago (Hokkaido, Honshu, and Shikoku). They clarified that *N. procyonoides* in Japan is monophyletic and the most divergent from the other Eurasian continental lineages. Although they did not infer the divergence time between lineages in the continent and Japan, the average pairwise difference in the transversional substitutions between the Japanese and continental lineages can be calculated to be 0.135 % based on the data of Kim et al. (2013), enabling me to estimate that the time for the origin of the raccoon dog lineage in Japan is 0.64 MYA based on the 0.21 % transversions/myr divergence rate estimated for the mustelid taxa in Sato et al. (2003), where the transversional substitutions were not shown to be affected by the saturation problem. The average pairwise distance between the most divergent lineages in Japan was also calculated to be 0.081 %, meaning that the earliest lineage diversification of *N. procyonoides* occurred 0.38 MYA in Japan. However, because the evolutionary rate in Sato et al. (2003) was based on the interspecific divergence, leading to the underestimation of the divergence rate and overestimation of the divergence time (Ho et al. 2005), the real divergence times might be younger than estimated.

Ursidae

The family Ursidae for bears and the giant panda is one of the large body-sized and charismatic taxa to which much attention has been paid for reasons of attractiveness and human–bear conflicts. There are only eight species in this family in the world and two of them exist in the Japanese Archipelago (Wozencraft 2005): one is the brown bear *Ursus arctos* in Hokkaido, and the other is the Asian black bear *Ursus thibetanus* in the HSK region. *U. arctos* is also distributed in the northern parts of Eurasia and America [therefore currently shown as a BP1 species, but treated in this study as a BP4 species because of the fossil evidence in Honshu (Kawamura 1994); Table 3.1], and *U. thibetanus* has a distribution in more southern areas in the Eurasian continent including the Oriental and Southwest Asian regions (BP7; Table 3.1). The phylogenetic relationships among the ursine species have been an evolutionary conundrum extensively debated to date and still remain to be clarified. Yu et al. (2007) and Krause et al. (2008) examined the whole mitochondrial genome and obtained the result with high reliability that *U. arctos* and the polar bear *Ursus maritimus* were the most closely related to each other, and that the two black bears, *U. thibetanus* and the American black bear *Ursus americanus*, were also sister species to each other. On the other hand, Pagès et al. (2008) also proposed a well-resolved and highly supported, but different, phylogeny estimated with 14 nuclear gene sequences, where in the clade of the genus *Ursus*, *U. arctos* and *U. maritimus* similarly formed a clade with *U. americanus* and *U. thibetanus* successively closely related to this clade, suggesting that the two black bears did not form a clade. Although such a mtDNA–nucDNA conflict in the ursid phylogeny should be addressed in a future study, the divergence times for the branching of *U. arctos* and *U. thibetanus* from the closest relatives were estimated to be 1.32 MYA and 5.19 MYA, respectively, in the analyses of the mitochondrial protein-coding gene sequences on the assumption of 12 MYA for the divergence between the giant panda and other bears (Yu et al. 2007). The time constraint of 12 MYA for the divergence between *Ailuropoda* and the other ursine lineage is consistent with the recent fossil finding in the lineage of the giant panda at 11–12 MYA (Abella et al. 2012). However, as I have noted repeatedly, the divergence times obtained here might be overestimates because of using the mitochondrial DNA with a calibration point too old for dating. Yu et al. (2007) also noted that their estimates are older than the fossil records and previous nuclear gene estimates. On the other hand, Krause et al. (2008) also estimated the dievergence times with the mitochondrial genome but different assumptions about the fossil calibrations (33.9 MYA for the divergence between Ursidae and Phocidae and 4.2–7.1 MYA for the basal ursine radiation). They showed 0.75–0.97 MYA and 3.66–4.69 MYA for the occurrence of lineages of *U. arctos* and *U. thibetanus*, respectively, which are not much different from but a little younger than estimates by Yu et al. (2007). Applying the same reasoning as in Yu et al. (2007), these dates are also results of overestimations because of the old calibration point (33.9 MYA), although the effect seems reduced by the younger calibration point (4.2–7.1 MYA). It should be noted that *U. maritimus* was demonstrated to be placed within the variation of *U. arctos*, so that the divergence times presented in both study does not reflect the emergence of *U. arctos*. Krause et al. (2008) estimated that the lineage including both *U. maritimus* and *U. arctos* diverged from the extinct cave bear *U. spelaeus* 2.41–3.11 MYA by using the ancient DNA technology.

It is still not clear from the dating information of only the interspecific divergence when *U. arctos* and *U. thibetanus* migrated into the Japanese Archipelago because the two species are not endemic to Japan. Therefore, the intraspecific variations should be assessed for clarifying the origins of these species in Japan. Using the mitochondrial *Cytb* and control region, Matsuhashi et al. (1999, 2001) detected three distinct lineages (central, eastern, and southern lineages) of *U. arctos* in Hokkaido that could have been established by independent migrations from the continent. The mitochondrial genome analyses also corroborated this result (Hirata et al. 2013). The central lineage is closely related to a widely expanded Holarctic lineage, the eastern lineage has close relatives in Russian Far East and Alaska, and the southern lineage shows phylogenetic affinity to the North American lineage (Korsten et al. 2009; Davison et al. 2011; Gus'kov et al. 2013; Hirata et al. 2013). On the basis of the mitochondrial genome and the ancient DNA (radiocarbon) calibration, Hirata et al. (2013) inferred that the divergence between the central lineage in Hokkaido and the clade composed of Eurasian, Sakhalin, and Alaskan lineages occurred 0.053 MYA. Unfortunately, they did not estimate the date for the origin of the eastern lineage in Hokkaido, only showing that the time to MRCA of the clade including the lineages in Hokkaido and Kuril (Etorofu and Kunashiri) islands was 0.042 MYA. Although a further analysis of the mitochondrial genome for the closely related Russian Far Eastern and Alaskan individuals would be needed, the Late Pleistocene origin for the eastern lineage in Hokkaido could be considered as suggested in other previous studies (Korsten et al. 2009; Davison et al. 2011). Hirata et al. (2013) also estimated that the southern lineage in Hokkaido diverged from the closely related American lineage 0.194 MYA, suggesting that the southern lineage first migrated into Hokkaido in the Middle Pleistocene when the Tsugaru Strait was not established. This time estimate is consistent with the palaeontological evidence that fossil remains of *U. arctos* were discovered from the Middle to Late Pleistocene layers in Honshu Islands, although currently no brown bears are found there (Kawamura et al. 1989; Kawamura 1994).

In contrast to *U. arctos*, the lineage of *U. thibetanus* in Japan would have migrated from the southern route via Korean Peninsula and Kyushu (albeit considered extinct in Kyushu now) as the distribution of the same species ranges in relatively southern areas in the Eurasian continent. Two papers could be mentioned to explore the origin of *U. thibetanus* in Japan (Ohnishi et al. 2009; Yasukochi et al. 2009). Ohnishi et al. (2009) examined the mitochondrial control region and found that there are three lineages (eastern, western, and southern lineages) among the black bear populations. Using the calibration point that the divergence time between *U. arctos* and *U. thibetanus* was 2.0–3.5 MYA, they estimated that *U. thibetanus* in Japan diverged from that in the continent 1.42–2.57 MYA and the time to the MRCA of three lineages detected in Japan was 0.295–0.583 MYA although they noted a concern about the estimated divergence time because of the uncertainty in the molecular clock. On the other hand, Yasukochi et al. (2009) estimated that *U. thibetanus* in Japan diverged from that in the continent 0.48 to 0.66 MYA in the Middle Pleistocene by using the mitochondrial *Cytb* gene and the calibration point of 1.2 MYA for the *U. arctos* and the cave bear *U. splaeus* divergence. However, the assumptive date for the calibration point (1.2 MYA) is not consistent with the recent estimate of their divergence (2.41–3.11 MYA; see above). If I take a brief proportion calculation, 0.48–0.66 MYA calculated with the 1.2 MYA for the *U. arctos* and *U. splaeus* can be translated into 0.96–1.71 MYA with 2.41–3.11 MYA for the calibration point, the range of which is overlapped with that in Ohnishi et al. (2009; 1.42–2.57 MYA). The corrected estimate (0.96–1.71 MYA) is more close to the fossil evidence that *U. thibetanus* was found around 0.50 MYA in Japan and also the land bridge is considered to have been formed in this age between Korean Peninsula and the Japanese Archipelago (Dobson and Kawamura 1998).

Mustelidae

Mustelidae is the most speciose family in the order Carnivora (59 species; Wozencraft 2005), showing a variety of ecological adaptations with aquatic, arboreal, fossorial, and terrestrial locomotors. Such ecological diversifications were demonstrated to have occurred in the Middle to Late Miocene after the mid-Miocene climatic optimum (ca. 15 MYA) and produced divergent lineages corresponding to the current subfamilies (Sato et al. 2012; Sato 2016; Sato and Wolsan 2016). There are seven indigenous, terrestrial, and extant mustelids in the Japanese archipelago (therefore, the exotic American mink *Neovison vison*, the aquatic sea otter *Enhydra lutris*, and the extinct Japanese otter *Lutra nippon* are not included), representing three subfamilies (Sato et al. 2012), arboreal Guloninae (two *Martes* species), fossorial Melinae (one *Meles* species), and terrestrial Mustelinae (four *Mustela* species). The distributions of mustelid species can be divided into four major biogeographic patterns (BP2, 4, 6, and 9; Table 3.1) (also see Sato 2013). The origin of the sable *Martes zibellina* in Hokkaido (BP2) has been inferred by using the mitochondrial DNA variations (Sato et al. 2011; Kinoshita et al. 2015) and a recombination rate in some nuclear genes (Ishida et al. 2013). Although there are some variations among the estimates from these studies, all supported the monophyly and the Late Pleistocene origin of the sable in Hokkaido.

The estimate for the divergence time between the Hokkaido lineage and the closest continental equivalent spanning western to eastern Russia was recently estimated to be 0.09 MYA on the basis of the mitochondrial *Nd2* gene sequences and the assumption that the divergence between *Martes foina* and the other *Martes* species occurred 3.045 MYA (the time to the MRCA of the Hokkaido individuals was estimated to be 0.04 MYA; Kinoshita et al. 2015). The time estimate and the distribution patterns are again in agreement with the hypothesis of the Tsugaru Strait barrier in the Late Pleistocene as *Sorex minutissimus*, *Sorex gracillimus*, *Apodemus peninsulae*, and *Myodes rutilus*. Excluding the artificially introduced populations in Hokkaido and Sado Islands, the Japanese marten *Martes melampus* is endemic to the HSK region (BP6; Table 3.1). It has been revealed through the phylogenetic analyses of the whole mitochondrial genome with detailed palaeontological information as calibration points that *M. melampus* diverged from the clade composed of *M. zibellina* and the pine marten *Martes martes* 1.0 to 1.1 MYA (Li et al. 2013; in particular, see this paper for the calibration details). It could therefore be stressed that *M. melampus* might have migrated into the Japanese Archipelago earlier than the congeneric species *M. zibellina* on Hokkaido, probably via Sakhalin, considering that the distributions of the closely related species (true martens) are all in northern Eurasia. Although the reason for the absence of *M. melampus* in Hokkaido is not clear, Ishida et al. (2013) implied the past interspecific hybridization in Hokkaido between *M. zibellina* and an entity closely related to *M. melmapus* and *M. americana*.

Establishment of the ermine or stoat *Mustela erminea* and the least weasel *Mustela nivalis* in the Japanese Archipelago has been considered a somewhat complicated. Although both species possess a similar distribution pattern (BP4; Table 3.1), the extent of intraspecific genetic variations of *M. nivalis* is much larger than *M. erminea* (Kurose et al. 2005). The former species also shows salient morphological diversity among local subspecies worldwide (Abramov and Baryshnikov 2000). Kurose et al. (2005) considered that such a contrast between *M. erminea* and *M. nivalis* resulted from the difference in their migration histories after the last glacial age. In their study, four haplotypes of *M. erminea* were found in Japan. Three of these haplotypes from Hokkaido and Honshu were closely related to Novgorod (western Russia) and Kazakhstan haplotypes, and the other one, from Honshu, to the Kamchatka (eastern Russia) haplotype. On the other hand, five haplotypes were detected from *M. nivalis* in Japan, four of which were clustered as a monophyletic Hokkaido lineage closely related to North American haplotypes, whereas the other one from Honshu showed close affinity with Russian haplotypes. Although almost all the relationships for these two species lineages were weakly supported, these results indicate multiple migrations of these two weasels into the Japanese Archipelago. Unfortunately, to date, the time scale has not been estimated for either species in Japan from molecular data. Dawson et al. (2014) examined intraspecific variations of *M. erminea* with two mitochondrial and four nuclear genes and showed with the *Cytb* gene variations that all the intraspecific diversifications occurred in the Late Pleistocene, although the Japanese lineages were not discussed in their study. Because they used the divergence rate calculated based on the geology of the Japanese islands, I could not use this information as independent evidence for the Late Pleistocene origin of *M. erminea* in Japan because of the circular argument. If I use the divergence rate of 1.90–2.68 %/myr obtained in the study of the Japanese weasel (Masuda et al. 2012), the extent of genetic differences between the Japanese and continental lineages in *M. erminea* and *M. nivalis* calculated for the data of Kurose et al. (2005) correspond to 0.13 to 0.39 MYA in the Middle Pleistocene and 0.45 to 1.02 MYA in the Early to Middle Pleistocene, respectively, meaning that *M. nivalis* first colonized the Japanese archipelago, followed by *M. erminea*. In contrast, it is confusing that fossil remains suggest that *M. erminea* was found in the Middle to Late Pleistocene, whereas *M. nivalis* is only in the Late Pleistocene in the HSK region (Kawamura et al. 1989).

The lineage of the Japanese weasel *Mustela itatsi*, endemic to the HSK region (BP6; Table 3.1), was inferred to have been generated 1.5–1.6 MYA (Sato et al. 2012) through a rapid diversification among *M. itatsi*, the Siberian weasel *M. sibirica*, and a clade of other mainly European species in the same genus (*M. eversmanii*, *M. lutreola*, *M. putorius*, and probably *M. nigripes*). Masuda et al. (2012) examined the intraspecific variations with the mitochondrial region and estimated using the divergence rate of 1.90–2.68 %/myr that the earliest divergence time between the most divergent lineages (Honshu vs. Shikoku-Kyushu) was 0.83–1.17 MYA. The fossil evidence suggests that *M. itatsi* was present in the Middle Pleistocene (0.43 MYA; Ogino et al. 2009). It is therefore considered that the origin and the diversification of *M. itatsi* in Japan lies in the Early Pleistocene. Except for the introduced populations, *M. sibirica* is only present in the Tsushima Islands in Japan (BP10; Table 3.1). Although the divergence time of the Tsushima population from the continental equivalent has not been assessed and remains to be elucidated, Masuda et al. (2012) showed that the Tsushima lineage diverged from the clade composed of the Korean and Russian haplotypes. The average pairwise sequence difference between these lineages (1.5 %) could be calculated into 0.56–0.80 MYA, suggesting that *M. sibirica* in Tsushima originated in the Middle Pleistocene.

The Japanese badger *Meles anakuma* is also endemic to the HSK region as are *Martes melampus* and *Mustela itatsi* (BP6, Table 3.1). The closest lineage was estimated to be the Asian badger *Meles leucurus*, inhabiting the eastern parts of the Eurasian continent (Marmi et al. 2006; Cerro et al. 2010; Tashima et al. 2011; Sato 2016), and their divergence time was calculated to be 0.5 MYA (Tashima et al. 2011), which is consistent with the fossil record (0.43 MYA; Ogino et al. 2009). In addition, Tashima et al. (2011) suggested that there were no genetic differentiations in the mitochondrial control region and the Y-chromosomal *Sry* gene among populations in Honshu, Shikoku, and Kyushu, probably formed by a rapid population expansion after the glacial period. They estimated that the differentiations among them occurred 0.11–0.23 MYA based on the divergence rate of 1.92 %/myr proposed in Marmi et al. (2006) and discussed that the time estimate of the diversification included the interglacial period before the last glacial period.

Cetartiodactyla

Bovidae

Bovidae is the most speciose artiodactyl family, including 40 genera and 143 species (Grubb 2005). Together with the chevrotain family Tragulidae, the pronghorn family Antilocapridae, the giraffe and okapi famlily Giraffidae, the deer family Cervidae, and the musk deer family Moschidae, they constitute Ruminantia, a species-rich clade in Artiodactyla (Hassanin et al. 2012). Only one bovid species, the Japanese serow *Capricornis crispus*, is indigenously and exclusively present in the HSK region of the Japanese archipelago (BP = 6; Table 3.1) (also see Ohdachi et al. 2015). Molecular phylogenetic research based on the mitochondrial genome sequences has suggested that *C. crispus* is the most closely related to the clade consisting of two congeneric species, the Chinese serow (or just the serow), *C. milneedwardsii*, and the Formosan serow *C. swinhoei* (Chikuni et al. 1995; Hassanin et al. 2012; Bibi 2013). It was suggested in the latter two studies that the divergence of *C. crispus* from the sister clade occurred around the Late Pliocene to the Early Pleistocene. Okumura (2004) examined the mitochondrial control region for the three *Capricornis* species (it should be noted that they used the name *C. sumatraensis* for the Chinese serow) and estimated on the basis of the divergence rate from the bovid homologous region (10.62 %/myr; Luftus et al. 1994) that *C. crispus* diverged from *C. swinhoei* in the age older than 1 MYA. Liu et al. (2013) also adopted the similar rate assumption of the mitochondrial control region and obtained an estimate of 0.85 MYA for the occurrence of the *C. crispus* lineage (Although their explanations for the evolutionary rate was so confusing because they noted both human and bovid evolutionary rates in their paper and in addition the citations for the bovid evolutionary rate were incorrect, I suppose that the rate 10.62 % indicated by their study should come from Luftus et al. 1994).

For the intraspecific phylogeographic analyses, Min et al. (2004) examined the mitochondrial *Cytb* gene for the Japanese serows collected from Honshu and Kyushu and detected five haplotypes. Although the extent of the sequence differences was demonstrated to be low, each haplotype showed a locality-specific trend to a certain degree. Unfortunately, they did not infer the time scale. Because no reliable evolutionary rate of the *Cytb* gene variations could be found for the bovid lineages from previous literature, I provided a tentative evolutionary rate by a brief proportion calculation. First, the average pairwise difference of the *Cytb* gene sequences between *C. crispus* and the continental *Capricornis* lineages can be calculated to be 6.5 % from the data of Min et al. (2004). Considering that the average pairwise genetic distances of the control region between *C. crispus* and the continental *Capricornis* lineages is 10.5 %, based on data of Hassanin et al. (2012), 6.5 % of the *Cytb* gene variation shows 61.9 % (6.5 × 100/10.5) of the control region variation. Simply applying the proportion to the 10.62 %/myr rate of the control region, the divergence rate of the *Cytb* gene could be calculated to be

6.57 %/myr. If I adopt the 6.57 %/myr divergence rate of the *Cytb* gene, the pairwise genetic distance between the two most divergent haplotypes (0.6 %) was calculated to be 0.09 MYA, suggesting that the MRCA of the Honshu and Kyushu lineages was present in the Late Pleistocene in the Japanese Archipelago. The diversification of the extant Japanese lineages in the Late Pleistocene period is consistent with the story that this species could not migrate into Hokkaido because of the presence of the Tsugaru Strait (Ohshima 1991).

Cervidae

Cervidae encompasses 51 species assigned into 19 genera, constituting the second largest family among artiodactyls (Grubb 2005). Two major subfamilial lineages were recognized as Cervinae and Capreolinae, and the Cervinae species were estimated to have diversified in Central Asia during the Miocene to Pliocene period, producing the most speciose *Cervus* lineages (Gilbert et al. 2006). There is only one species, *Cervus nippon*, in the Japanese Archipelago, naturally distributed across the major islands except for the Ryukyu region with the same species observed in the continental East and Southeast Asia and Taiwan (BP = 4; Table 3.1) (also see Ohdachi et al. 2015). Molecular phylogenetic studies have clarified that the species most closely related to *C. nippon* is the red deer, *Cervus elaphus*, distributed worldwide in the Holarctic region, and the white-lipped deer *Cervus* (*Przewalskium*) *albirostris*, found in continental East Asia (Gilbert et al. 2006; Hassanin et al. 2012). Although the exact phylogenetic relationships among them remains to be clarified, Gilbert et al. (2006) indicated that the diversification of these lineages occurred around 1.5 MYA in the analyses of two mitochondrial (*Cytb* and *Co2*) and two nuclear (*αLalb* and *Prkci*) genes.

As regards the intraspecific variation of *C. nippon* in the Japanese Archipelago, it has been demonstrated that there are two major mitochondrial DNA lineages geographically demarcated by a borderline in southern Honshu between Hyogo and Yamaguchi Prefectures (in the Chugoku district), which are called the northern and southern lineages (Tamate et al. 1998; Nagata et al. 1999). Assuming the 10.6 %/myr divergence rate of the mitochondrial control region sequences (Luftus et al. 1994), Nagata et al. (1999) estimated that divergence time among the Chinese conspecific, the northern Japanese, and the southern Japanese lineages was about 0.30 MYA in the Middle Pleistocene. Because the divergence time between northern and southern Japanese lineages was the oldest, they interpreted that the divergence occurred in the continent and that these two Japanese lineages independently migrated into the Japanese Islands. The Middle Pleistocene origin of *C. nippon* in the continent and subsequent migrations into the Japanese Archipelago are consistent with the fossil records of Kawamura et al. (1989) that the Japanese sika deer was first found in the Late Pleistocene.

Suidae

The family Suidae contains 19 species classified into 5 genera (Grubb 2005) and includes the wild boar *Sus scrofa*, which is an ancestor of the pig, an important domesticated animal strongly related to human life. Recent molecular phylogenetic analyses with the mitochondrial genome revealed that the Suidae and the closely related peccary family Tayassuidae constitute the most basal lineage within the Cetartiodactyla phylogeny (Hassanin et al. 2012). *S. scrofa* is a species widely distributed in the Eurasian continent and northern Africa (Grubb 2005) showing two major lineages in Europe and Asia, each having independently produced domestic pigs (Giuffra et al. 2000; Kijas and Anderson 2001). The occurrence of the *S. scrofa* lineage was estimated to have occurred 4.2 MYA in the Pliocene based on the autosomal genome sequences with millions of single-nucleotide polymorphism (SNP) data produced by the next-generation sequencer and on the fossil records, although some interspecific hybridizations were detected between *S. scrofa* and other closely related Southeast Asian species (Frantz et al. 2013). *S. scrofa* also exists in the major Japanese islands, except for Hokkaido (BP8; Table 3.1) (also see Ohdachi et al. 2015). HSK and the Ryukyu regions harbor different subspecies, the Japanese wild boar *S. s. leucomystax* and the Ryukyu wild boar *S. s. riukiuanus*, respectively (Ohdachi et al. 2015). It has been demonstrated with mitochondrial DNA variations that these two subspecies could have probably originated from different source populations in continental Eurasia (Okumura et al. 1996, 2001; Watanobe et al. 1999, 2003; Hongo et al. 2002). Watanobe et al. (2003) showed by examining the mitochondrial control region that the Japanese wild boar in HSK is phylogenetically closely related to the East Asian lineages in the continent and is not monophyletic because some northeast Asian haplotypes are included within this Japanese wild boar clade. It was estimated in the same study that the lineage of the Japanese wild boars in the HSK region diverged 0.14 to 0.25 MYA in the Middle Pleistocene from the continental East Asian lineage on the basis of the assumption that the divergence time between European and Asian wild boars was 0.5 to 0.9 MYA (Giuffra et al. 2000; Kijas and Anderson 2001). It should however be noted here that, as Giuffra et al. (2000) based their time estimations on the evolutionary rate from Brown et al. (1979; RFLP data for primates), the divergence time of 0.5 MYA between Asian and European wild boars may not be accurate. In addition, Frantz et al. (2013) estimated with genome sequencing that the divergence was much older (1.2 MYA) and relatively close to that of Kijas and Anderson (2001; 0.9 MYA). If I adopt the average (1.05 MYA) between 1.2 MYA and 0.9 MYA, the divergence of the Japanese wild boar would have taken place 0.29 MYA, also in the Middle Pleistocene. It has been demonstrated that there are at least three lineages among the Japanese wild boars (*S. s. leucomystax*), which would have been established multiple independent migration events (Ishiguro et al. 2008). On the other hand, using the mitochondrial control region, Hongo et al. (2002) and Ishiguro et al. (2008) suggested the close affinity between Ryukyu and Vietnamese individuals, which implies the migrations of the Ryukyu wild boar from the southern routes. However, the supportive value for the clade was extremely low and therefore such an affinity should be viewed as preliminary. Although Watanobe et al. (2003) did not examine the Vietnamese individuals, they estimated on the basis of 0.5–0.9 MYA for the European/Asian wild boar divergence that the Ryukyu lineage diverged 0.31–0.57 MYA from the other Asian lineage including the lineages of the Japanese wild boars in the HSK region. If I apply 1.05 MYA for the calibration points as above, the Ryukyu lineage was estimated to have branched off 0.66 MYA. There should, however, be a more closely related and still unidentified lineage in the continent such as the Vietnamese lineage because fossil evidence suggested that the wild boar is likely to have migrated into the Ryukyu Islands 0.018 MYA (Hasegawa 1980), which is also consistent with the geology of the Ryukyu Islands (Kimura 2000). Unfortunately, I could not calculate the divergence time between the Ryukyu and the Vietnamese lineages because there are no sequences of the Ryukyu endemic M16–M20 D-loop haplotypes used in Hongo et al. (2002) and Ishiguro et al. (2008) in the DNA database. Watanobe et al. (1999) showed that Amami–Oshima, Okinawajima, and Iriomotejima Islands in the Ryukyu region each possess an island-specific haplogroup (or haplotype) of the combined mitochondrial *Cytb* gene and control region, although no time scale was inferred.

References

Abella J, Alba DM, Robles JM, Valenciano A, Rotgers C, Carmona R, Montoya P, Morales J (2012) *Kretzoiarctos* gen. nov., the oldest member of the giant panda clade. PLoS One 7: e48985

Abramov AV, Baryshnikov GF (2000) Geographic variation and intraspecific taxonomy of weasel *Mustela nivalis* (Carnivora, Mustelidae). Zoosyst Rossica 8:365–402

Abramson NI, Petrova TV, Dokuchaev NE, Obolenskaya EV, Lissovsky AA (2012) Phylogeography of the gray red-backed vole *Craseomys rufocanus* (Rodentia: Cricetidae) across the distribution range inferred from nonrecombining molecular markers. Russ J Theriol 11:137–156

Aimi M (2002) The oldest fossil macaque from Japan. Primates Res 18:329–245 (in Japanese with English summary)

Bannikova AA, Lebedev VS, Lissovsky AA, Matrosova V, Abramson NI, Obolenskaya EV, Tesakov AS (2010) Molecular phylogeny and evolution of the Asian lineage of vole genus *Microtus* (Rodentia: Arvicolinae) inferred from mitochondrial cytochrome *b* sequence. Biol J Linn Soc 99:595–613

Bardeleben C, Moore RL, Wayne RK (2005) A molecular phylogeny of the Canidae based on six nuclear loci. Mol Phylogenet Evol 37:815–831

Benton MJ, Donoghue PC (2007) Palaeontological evidence to date the tree of life. Mol Biol Evol 24:26–53

Bibi F (2013) A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. BMC Evol Biol 13:166

Bininda-Emonds ORP, Gittleman JL, Purvis A (1999) Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biol Rev Camb Philos Soc 74:143–175

Brown WM, George M Jr, Wilson AC (1979) Rapid evolution of animal mitochondrial DNA. Proc Natl Acad Sci USA 76:1967–1971

Brunhoff C, Galbreath KE, Fedorov VB, Cook JA, Jaarola M (2003) Holarctic phylogeography of the root vole (*Microtus oeconomus*): implication for late Quaternary biogeography of high latitudes. Mol Ecol 12:957–968

Cardillo M, Gittleman JL, Purvis A (2008) Global patterns in the phylogenetic structure of island mammal assemblages. Proc R Soc B 275:1549–1556

Carleton MD, Gardner AL, Pavlinov IY, Musser GG (2014) The valid generic name for red-backed voles (Muroidea: Cricetidae: Arvicolinae): restatement of the case for *Myodes* Pallas, 1811. J Mammal 95:943–959

Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR (1997) Global vegetation change through the Miocene/Pliocene boundary. Nature (Lond) 389:153–158

Cerro ID, Marmi J, Ferrando A, Chashchin P, Taberlet P, Bosch M (2010) Nuclear and mitochondrial phylogenies provide evidence for four species of Eurasian badgers (Carnivora). Zool Scr 39:415–425

Chikuni K, Mori Y, Tabata T, Saito M, Monma M, Kosugiyama M (1995) Molecular phylogeny based on the k-casein and cytochrome b sequences in the mammalian suborder Ruminantia. J Mol Evol 41:859–866

Chu J-H, Lin Y-S, Wu H-Y (2007) Evolution and dispersal of three closely related macaque species *Macaca mulatta*, *M. cyclopis*, and *M. fuscata*, in the eastern Asia. Mol Phylogenet Evol 43:418–429

Conroy CJ, Cook JA (2000) Molecular systematics of a Holarctic rodent (*Microtus*: Muridae). J Mammal 81:344–359

Cook JA, Runck AM, Conroy CJ (2004) Historical biogeography at the crossload of the northern continents: molecular phylogenetics of red-backed voles (Rodentia: Arvicolinae). Mol Phylogenet Evol 30:767–777

Cooper N, Rodríguez J, Purvis A (2008) A common tendency for phylogenetic overdispersion in mammalian assemblages. Proc R Soc B 275:2031–2037

Davison J, Ho SYW, Bray SC, Korsten M, Tammeleht E, Hindrikson M, Østbye K, Østbye E, Lauritzen SE, Austin J, Cooper A, Saarma U (2011) Late-Quaternary biogeographic scenarios for the brown bear (*Ursus arctos*), a wild mammal model species. Quat Sci Rev 30:418–430

Dawson NG, Hope AG, Talbot SL, Cook JA (2014) A multilocus evaluation of ermine (*Mustela erminea*) across the Holarctic, testing hypotheses of Pleistocene diversification in response to climate change. J Biogeogr 41:464–475

Dayan T, Simberloff D (2005) Ecological and community-wide character displacement: the next generation. Ecol Lett 8:875–894

Dobson M (1994) Patterns of distribution in Japanese land mammals. Mammal Rev 24:91–111

Dobson M, Kawamura Y (1998) Origin of the Japanese land mammal fauna: allocation of extant species to historically-based categories. Quat Res 37:385–395

Dubey S, Zaitsev M, Cosson J-F, Abdukadier A, Vogel P (2006) Pliocene and Pleistocene diversification and multiple refugia in a Eurasian shrew (*Crocidura suaveolens* group). Mol Phylogenet Evol 38:635–647

Dubey S, Salamin N, Ohdachi SD, Barrière P, Vogel P (2007) Molecular phylogenetics of shrews (Mammalia: Soricidae) reveal timing of transcontinental colonizations. Mol Phylogenet Evol 44:126–137

Dubey S, Salamin N, Ruedi M, Barrière P, Colyn M, Vogel P (2008) Biogeographic origin and radiation of the Old World crocidurine shrews (Mammalia: Soricidae) inferred from mitochondrial and nuclear genes. Mol Phylogenet Evol 48:953–963

Emerson BC, Gillespie RG (2008) Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol Evol 23:619–630

Endo H, Tsuchiya K (2006) A new species of Ryukyu spiny rat, *Tokudaia* (Muridae: Rodentia), from Tokunoshima Island, Kagoshima Prefecture, Japan. Mamm Study 31:47–57

Fedorov VB, Stenseth NC (2001) Glacial survival of the Norwegian lemming (*Lemmus lemmus*) in Scandinavia: inference from mitochondrial DNA variation. Proc R Soc B 268:809–814

Frankham R, Ballou JD, Briscoe DA (2010) Introduction to conservation genetics, 2nd edn. Cambridge University Press, Cambridge, 642 pp

Frantz LAF, Schraiber JG, Madsen O, Megens H-J, Bosse M, Paudel Y, Semiadi G, Meijaard E, Li N, Crooijmans RPMA, Archibald AL, Slatkin M, Schook LB, Larson G, Groenen MAM (2013) Genome sequencing reveals fine scale diversification and reticulation history during speciation in *Sus*. Genome Biol 14:R107

Fumagalli L, Taberlet P, Stewart DT, Gielly L, Hausser J, Vogel P (1999) Molecular phylogeny and evolution of *Sorex* shrews (Soricidae: Insectivora) inferred from mitochondrial DNA sequence data. Mol Phylogenet Evol 11:222–235

Gerhold P, Cahill JF Jr, Winter M, Bartish IV, Prinzing A (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). Funct Ecol 29:600–614

Gilbert C, Ronquist A, Hassanin A (2006) Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): systematics, morphology, and biogeography. Mol Phylogenet Evol 40:101–117

Gillespie R (2004) Community assembly through adaptive radiation in Hawaiian spiders. Science 303:356–359

Gissi C, Reyes A, Pesole G, Saccone C (2000) Lineage-specific evolutionary rate in mammalian mtDNA. Mol Biol Evol 17:1022–1031

Giuffra E, Kijas JMH, Amarger V, Carlborg Ö, Jeon J-T, Anderson L (2000) The origin of the domestic pig: independent domestication and subsequent introgression. Genetics 154:1785–1791

Grill A, Amori G, Aloise G, Lisi I, Tosi G, Wauters LA, Randi E (2009) Molecular phylogeography of European *Sciurus vulgaris*: refuge within refugia? Mol Ecol 18:2687–2699

Groves C (2005) Order Primates. In: Wilson E, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 111–184

Grubb P (2005) Order Artiodactyla. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 637–722

Gus'kov VY, Shermet'eva IN, Seredkin IV, Kryukov AP (2013) Mitochondrial cytochrome *b* gene variation in brown bear (*Ursus arctos* Linnaeus, 1758) from southern part of Russian Far East. Russ J Genet 49:1213–1218

Han S-H, Iwasa MA, Ohdachi SD, Oh H-S, Suzuki H, Tsuchiya K, Abe H (2002) Molecular phylogeny of *Crocidura* shrews in northeastern Asia: a special reference to specimens on Cheju Island, South Korea. Acta Theriol 47:369–379

Hasegawa Y (1980) Notes on vertebrate fossils from the late Pleistocene to Holocene of Ryukyu Islands, Japan. Quat Res 18:263–267 (in Japanese with English abstract)

Hassanin A, Delsuc E, Ropiquet A, Hammer C, van Vuuren BJ, Matthee C, Ruiz-Garcia M, Catzeflis F, Areskoug V, Nguyen TT, Couloux A (2012) Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. C R Biol 335:32–50

Hata S (2011) Nesting characteristics of harvest mice (*Micromys minutus*) in three types of Japanese grasslands with different inundation frequencies. Mamm Study 36:49–53

Hayasaka K, Fujii K, Horai S (1996) Molecular phylogeny of macaques: implications of nucleotide sequences from an 896-base pair region of mitochondrial DNA. Mol Biol Evol 13:1044–1053

He K, Li Y-J, Brandley MC, Lin L-K, Wang Y-X, Zhang Y-P, Jiang X-L (2010) A multi-locus phylogeny of Nectogalini shrew and influences of the paleoclimate on speciation and evolution. Mol Phylogenet Evol 56:734–746

He K, Shinohara A, Jiang X-L, Campbell KL (2014) Multilocus phylogeny of talpine moles (Talpini, Talpidae, Eulipotyphla) and its implications for systematics. Mol Phylogenet Evol 70:513–521

Hedge SB (2006) Palaeogeography of the Antilles and origin of West Indian terrestrial vertebrates. Ann Mo Bot Gard 93:231–244

Herron MD, Castoe TA, Parkinson CL (2004) Sciulid phylogeny and the paraphyly of Holarctic ground squirrels (*Spermophilus*). Mol Phylogenet Evol 31:1015–1030

Hirata D, Mano T, Abramov AV, Baryshnikov GF, Kosintsev PA, Vorobiev AA, Raichev EG, Tsunoda H, Kaneko Y, Murata M, Fukui D, Masuda R (2013) Molecular phylogeography of the brown bear (*Ursus arctos*) in northeastern Asia based on analyses of complete mitochondrial DNA sequences. Mol Biol Evol 30:1644–1652

Ho SYW, Phillips MJ, Cooper A, Drummond AJ (2005) Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. Mol Biol Evol 22:1561–1568

Hoffmann RS, Smith AT (2005) Order Lagomorpha. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 185–211

Holden ME (2005) Order Primates. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 819–841

Hongo H, Ishiguro N, Watanobe T, Shigehara N, Anezaki T, Long VT, Binh DV, Tien NT, Nam NH (2002) Variation in mitochondrial DNA of Vietnamese pigs: relationships with Asian domestic pigs and Ryukyu wild boars. Zool Sci 19:1329–1335

Hope AG, Waltari E, Dokuchaev NE, Abramov S, Dupal T, Tsvetkova A, Henttonen H, MacDonald SO, Cook JA (2010) High-latitude diversification within Eurasian least shrews and Alaska tiny shrews (Soricidae). J Mammal 91:1041–1057

Hope AG, Ho SYW, Malaney JL, Cook JA, Talbot SL (2014) Accounting for rate variation among lineages in comparative demographic analyses. Evolution 68–69:2689–2700

Hutterer R (2005) Order Soricomorpha. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 220–311

Inoue T, Nonaka N, Mizuno A, Morishima Y, Sato H, Katakura K, Oku Y (2007) Mitochondrial DNA phylogeography of the red fox (*Vulpes vulpes*) in northern Japan. Zool Sci 24:1178–1186

Irwin DM, Kocher TD, Wilson AC (1991) Evolution of the cytochrome *b* gene of mammals. J Mol Evol 32:128–144

Ishida K, Sato JJ, Kinoshita G, Hosoda T, Kryukov AP, Suzuki H (2013) Evolutionary history of the sable (*Martes zibellina brachyura*) on Hokkaido inferred from mitochondrial *Cytb* and nuclear *Mc1r* and *Tcf25* gene sequences. Acta Theriol 58:13–24

Ishiguro N, Sasaki M, Iwasa M, Shigehara N, Hongo H, Anezaki T, Long VT, Lan TB, Long PT (2008) mtDNA variation in Vietnamese pigs, with particular emphasis on the genetic relationship between wild boars from Vietnam and the Ryukyu Islands. Mamm Study 33:51–58

Iwasa MA, Abe H (2006) Colonization history of the Japanese water shrew *Chimarrogale platycephala*, in the Japanese Islands. Acta Theriol 51:29–38

Iwasa MA, Suzuki H (2002) Evolutionary networks of maternal and paternal gene lineages in voles (*Eothenomys*) endemic to Japan. J Mammal 83:852–865

Iwasa MA, Suzuki H (2003) Intra- and interspecific genetic complexity of two *Eothenomys* species in Honshu, Japan. Zool Sci 20:1305–1313

Jaarola M, Martínková N, Gündüz I, Brunhoff C, Zima J, Nadachowski A, Amori G, Bulatova NS, Chondropoulos B, Fraguedakis-Tsolis S, González-Esteban J, José López-Fuster M, Kandaurov AS, Kefelioğlu H, da Luz Mathias M, Villate I, Searle JB (2004) Molecular phylogeny of the speciose vole genus *Microtus* (Arvicolinae, Rodentia) inferred from mitochondrial DNA sequences. Mol Phylogenet Evol 33:647–663

Johnson WE, Eizirik E, Pecon-Slattery JP, Murphy WJ, Antunes A, Teeling E, O'Brien SJ (2006) The late Miocene radiation of modern Felidae: a genetic assessment. Science 311:73–77

Kaneko Y (2006) The taxonomy of Japanese Muridae (Mammalia, Rodentia): from the view point of biogeography. University of Tokyo Press, Tokyo, 302 pp (in Japanese)

Kawai K, Hailer F, de Guia AP, Ichikawa H, Saitoh T (2013) Refugia in glacial ages led to the current discontinuous distribution patterns of the dark red-backed vole *Myodes rex* on Hokkaido, Japan. Zool Sci 30:642–650

Kawamoto Y, Shotake T, Nozawa K, Kawamoto S, Tomari K, Kawai S, Shirai K, Morimitsu Y, Takagi N, Akaza H, Fujii H, Hagihara K, Aizawa K, Akachi S, Oi T, Hayaishi S (2007) Postglacial population expansion of Japanese macaques (*Macaca fuscata*) inferred from mitochondrial DNA phylogeography. Primates 48:27–40

Kawamura Y (1988) Quaternary rodents faunas in the Japanese islands (Part 1). Memoirs of the Faculty of Science, Kyoto Unviersity. Ser Geol Miner 53:31–348

Kawamura Y (1991) Quaternary mammalian faunas in the Japanese islands. Quat Res 30:213–220

Kawamura Y (1994) Late Pleistocene to Holocene mammalian faunal succession in the Japanese Islands, with comments on the late Quaternary extinctions. Archaeozoologia VI/2:7–22

Kawamura Y (1998) Immigration of mammals into the Japanese Islands during the quaternary. Quat Res 37:251–257 (in Japanese with English abstract)

Kawamura Y, Kamei T, Taruno H (1989) Middle and Late Pleistocene mammalian faunas in Japan. Quat Res 28:317–326 (in Japanese with English abstract)

Kijas JM, Anderson L (2001) A phylogenetic study of the origin of the domestic pig estimated from the near-complete mtDNA genome. J Mol Evol 52:302–308

Kim S-I, Park S-K, Lee H, Oshida T, Kimura J, Nguyen ST, Sashika M, Min M-S (2013) Phylogeography of Korean raccoon dogs: implications of peripheral isolation of a forest mammal in East Asia. J Zool 290:225–235

Kimura M (2000) Paleogeography of the Ryukyu Islands. Tropics 10:5–24

Kinoshita G, Nunome M, Han S-H, Hirakawa H, Suzuki H (2012) Ancient colonization and within-island vicariance revealed by mitochondrial DNA phylogeography of the mountain hare (*Lepus timidus*) in Hokkaido, Japan. Zool Sci 29:776–785

Kinoshita G, Sato JJ, Meschersky IG, Pishchulina SL, Simakin LV, Rozhnov VV, Malyarchuk B, Derenko M, Denisova G, Frisman LV, Kryukov AP, Hosoda T, Suzuki H (2015) Colonization history of the sable *Martes zibellina* (Mammalia, Carnivora) on the marginal peninsula and islands in northeastern Eurasia. J Mammal 96:172–184

Kirihara T, Shinohara A, Tsuchiya K, Harada M, Kryukov AP, Suzuki H (2013) Spatial and temporal aspects of occurrence of *Mogera* species in the Japanese Islands inferred from mitochondrial and nuclear gene sequences. Zool Sci 30:267–281

Kohli BA, Speer KA, Kilpatric CW, Batsaikhan N, Damdinbaza D, Cook JA (2014) Multilocus systematics and non-punctuated evolution of Holarctic Myodini (Rodentia: Arvicolinae). Mol Phylogenet Evol 76:18–29

Kohli BA, Fedorov VB, Waltari E, Cook JA (2015) Phylogeography of a Holarctic rodent (*Myodes rutilus*): testing high-latitude biogeographical hypotheses and the dynamic of range shifts. J Biogeogr 42:377–389

Korsten M, Ho SYW, Davison J, Pahn B, Vulla E, Roht M, Tumanov IL, Kojola I, Anderson-Lilley Z, Ozolins J, Pilot M, Mertzanis Y, Giannakopoulos A, Vorobiev AA, Markov NI, Saveljev AP, Lyapunova EA, Abramov AV, Mannil P, Valdmann H, Pazetnov SV, Pazetnov VS, Rokov AM, Saarma U (2009) Sudden expansion of a single brown bear maternal lineage across northern continental Eurasia after the last ice age: a general demographic model for mammals? Mol Ecol 18:1963–1979

Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. Funct Ecol 29:592–599

Krause J, Under T, Noçon A, Malaspinas A-S, Kolokotronis S-O, Stiller M, Soibelzon L, Spriggs H, Dear DH, Briggs AW, Bray SCE, O'Brien SJ, Rabeder G, Matheus P, Cooper A, Slatkin M, Pääbo S, Hofreiter M (2008) Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene–Pliocene boundary. BMC Evol Biol 8:220

Kueffer C, Drake DR, Fernández-Palacios JM (2014) Island biology: looking towards the future. Biol Lett 10:20140719

Kurose N, Abramov AV, Masuda R (2005) Comparative phylogeography between the ermine *Mustela erminea* and the least weasel *M. nivalis* of Palaearctic and Nearctic regions, based on analysis of mitochondrial DNA control region sequences. Zool Sci 22:1069–1078

Kutschera VE, Lecomte N, Janke A, Selva N, Sokolov AA, Haun T, Steyer K, Nowak C, Hailer F (2013) A range-wide synthesis and timeline for phylogeographic events in the red fox (*Vulpes vulpes*). BMC Evol Biol 13:114

Lanier HC, Olson LE (2009) Inferring divergence times within pikas (*Ochotona* spp.) using mtDNA and relaxed molecular dating techniques. Mol Phylogenet Evol 53:1–12

Lebedev VS, Bannikova AA, Tesakov AS, Abramson NI (2007) Molecular phylogeny of the genus *Alticola* (Cricetidae, Rodentia) as inferred from the sequence of the cytochrome *b* gene. Zool Scr 36:547–563

Lee M-Y, Park S-K, Hong Y-J, Kim Y-J, Voloshina I, Myslenkov A, Saveljev AP, Choi T-Y, Piao R-Z, An J-H, Lee M-H, Min M-S (2008) Mitochondrial genetic diversity and phylogenetic relationships of Siberian flying squirrel (*Pteromys volans*) populations. Anim Cells Syst 12:269–277

Li S, He K, Yu F-H, Yang Q-S (2013a) Molecular phylogeny and biogeography of *Petaurista* inferred from the cytochrome *b* gene, with implications for the taxonomic status of *P. caniceps*, *P. marica* and *P. sybilla*. PLoS One 8:e70461

Li B, Wolsan M, Wu D, Zhang W, Xu Y, Zeng Z (2013b) Mitochondrial genome reveal the pattern and timing of marten (*Martes*), wolverine (*Gulo*), and fisher (*Pekania*) diversification. Mol Phylogenet Evol 80:156–164

Lindblad-Toh K, Wade CM, Mikkelsen TS, Karlsson EK, Jaffe DB, Kamal M, Clamp M, Chang JL, Kulbokas EJ, Zody MC, Mauceli E, Xie XH, Breen M, Wayne RK, Ostrander EA, Ponting CP, Galibert F, Smith DR, deJong PJ, Kirkness E, Alvarez P, Biagi T, Brockman W, Butler J, Chin CW, Cook A, Cuff J, Daly MJ, DeCaprio D, Gnerre S, Grabherr M, Kellis M, Kleber M, Bardeleben C, Goodstadt L, Heger A, Hitte C, Kim L, Koepfli KP, Parker HG, Pollinger JP, Searle SMJ, Sutter NB, Thomas R, Webber C, Lander ES, Plat BIGS (2005) Genome sequence, comparative analysis and haplotype structure of the domestic dog. Nature (Lond) 438:803–819

Lissovsky AA, Ivanova NV, Borisenko AV (2007) Molecular phylogenetics and taxonomy of the subgenus *Pika* (*Ochotona*, Lagomorpha). J Mammal 88:1195–1204

Liu W, Yao Y-F, Yu Q, Ni Q-Y, Zhang M-W, Yang J-D, Mai M-M, Xu H-L (2013) Genetic variation and phylogenetic relationship between three serow species of the genus *Capricornis* based on the complete mitochondrial DNA control region sequences. Mol Biol Rep 40:6793–6802

Liu Z, Li B, Ma J, Zheng D, Xu Y (2014) Phylogeography and genetic diversity of the red squirrel (*Sciurus vulgaris*) in China: implications for the species' postglacial expansion history. Mamm Biol 79:247–253

Luftus RT, Machugh DE, Bradley DG, Sharp PM, Cunningham P (1994) Evidence for two independent domestications of cattle. Proc Natl Acad Sci USA 91:2757–2761

Luo J, Yang D, Suzuki H, Wang Y, Chen W-J, Campbell KL, Zhang Y-P (2004) Molecular phylogeny and biogeography of Oriental voles: genus *Eothenomys* (Muridae, Mammalia). Mol Phylogenet Evol 33:349–362

Marmi J, Bertranpetit J, Terradas J, Takenaka O, Domingo-Roura X (2004) Radiation and phylogeography in the Japanese macaque, *Macaca fuscata*. Mol Phylogenet Evol 30:676–685

Marmi J, Lopéz-Giráldez F, Macdonald DW, Calafell F, Zholnerovskaya E, Domingo-Roura X (2006) Mitochondrial DNA reveals a strong phylogeographic structure in the badger across Eurasia. Mol Ecol 15:1007–1020

Masuda R, Yoshida MC (1995) The Japanese wildcats, the Tsushima cat and the Iriomote cat, show the same mitochondrial DNA lineage as the leopard cat *Felis bengalensis*. Zool Sci 12:655–659

Masuda R, Yoshida MC, Shinyashiki F, Bando G (1994) Molecular phylogenetic status of the Iriomote cat *Felis iriomotensis* inferred from mitochondrial DNA sequence analysis. Zool Sci 11:597–604

Masuda R, Kurose N, Watanabe S, Abramov AV, Han SH, Lin LK, Oshida T (2012) Molecular phylogeography of the Japanese weasel, *Mustela itatsi* (Carnivora: Mustelidae), endemic to the Japanese islands, revealed by mitochondrial DNA analysis. Biol J Linn Soc 107:307–321

Matson CW, Baker RJ (2001) DNA sequence variation in the mitochondrial control region of red-backed voles (*Clethrionomys*). Mol Biol Evol 18:1494–1501

Matsuhashi T, Masuda R, Mano T, Yoshida MC (1999) Microevolution of the mitochondrial DNA control region in the Japanese brown bear (*Ursus arctos*) population. Mol Biol Evol 16:676–684

Matsuhashi T, Masuda R, Mano T, Murata K, Aiurzaniin A (2001) Phylogenetic relationships among worldwide populations of the brown bear *Ursus arctos*. Zool Sci 18:1137–1143

Matthee CA, van Vuuren BJ, Bell D, Robinson TJ (2004) A molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. Syst Biol 53:433–447

McKay BD (2012) A new timeframe for the diversification of Japan's mammals. J Biogeogr 39:1134–1143

Mercer JM, Roth VL (2003) The effects of Cenozoic global change on squirrel phylogeny. Science 299:1568–1572

Michaux JR, Chevret P, Filippucci M-G, Macholan M (2002) Phylogeny of the genus *Apodemus* with a special emphasis on the subgenus *Sylvaemus* using the nuclear IRBP gene and two mitochondrial markers: cytochrome *b* and 12S rRNA. Mol Phylogenet Evol 23:123–136

Millien-Parra V, Jaeger J-J (1999) Island biogeography of the Japanese terrestrial mammal assembladges: an example of a relict fauna. J Biogeogr 26:959–972

Min M-S, Okumura H, Jo D-J, Hwa J, Kim K-S, Kimm C-B, Shin N-S, Lee M-H, Han C-H, Voloshina IV, Lee H (2004) Molecular phylogenetic status of the Korean goral and Japanese serow based on partial sequences of the mitochondrial cytochrome *b* gene. Mol Cells 17:365–372

Motokawa M (2000) Biogeography of living mammals in the Ryukyu Islands. Tropics 10:63–71

Motokawa M, Suzuki H, Harada M, Lin L-K, Koyasu K, Oda S (2000) Phylogenetic relationships among east Asian species of *Crocidura* (Mammalia, Insectivora) inferred from mitochondrial cytochrome *b* gene sequences. Zool Sci 17:497–504

Motokawa M, Lin L-K, Motokawa J (2003) Morphological comparison of Ryukyu mouse *Mus caroli* (Rodentia: Muridae) populations from Okinawajima and Taiwan. Zool Stud 42:258–267

Murata C, Yamada F, Kawauchi N, Matsuda Y, Kuroiwa A (2010) Multiple copies of SRY on the large Y chromosome of the Okinawa spiny rat, *Tokudaia muenninki*. Chromosome Res 18:623–634

Musser GG, Carleton MD (2005) Superfamily Muloidea. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 894–1531

Nabholz B, Glémin S, Galtier N (2008) Strong variations of mitochondrial mutation rate across mammals: the longevity hypothesis. Mol Biol Evol 25:120–130

Nagata J, Masuda R, Tamate HB, Hamasaki S, Ochiai K, Asada M, Tatsuzawa S, Suda K, Tado H, Yoshida MC (1999) Two genetically distinct lineages of the sika deer, *Cervus nippon*, in Japanese Islands: comparison of mitochondrial D-loop region sequences. Mol Phylogenet Evol 13:511–519

Narwani A, Matthews B, Fox J, Venail P (2015) Using phylogenetics in community assembly and ecosystem functioning research. Funct Ecol 29:589–591

Neall VE, Trewick SA (2008) The age and origin of the Pacific islands: a geological overview. Philos Trans R Soc B 363:3293–3308

Niu Y, Wei F, Xiaoming ML, Feng Z (2004) Phylogeny of pikas (Lagomorpha, *Ochotona*) inferred from mitochondrial cytochrome *b* sequences. Folia Zool 53:141–155

Nunome M, Yasuda SP, Sato JJ, Vogel P, Suzuki H (2007) Phylogenetic relationships and divergence times among dormice (Rodentia, Gliridae) based on three nuclear genes. Zool Scr 36:537–546

Nunome M, Torii H, Matsuki R, Kinoshita G, Suzuki H (2010) The influence of Pleistocene refugia on the evolutionary history of the Japanese hare, *Lepus brachyurus*. Zool Sci 27:746–754

Nunome M, Kinoshita G, Tomozawa M, Torii H, Matsuki R, Yamada F, Matsuda Y, Suzuki H (2014) Lack of association between winter coat colour and genetic population structure in the Japanese hare, *Lepus brachyurus* (Lagomorpha: Leporidae). Biol J Linn Soc 111:761–776

Obolenskaya EV, Lee M-Y, Dokuchaev NE, Oshida T, Lee M-S, Lee H, Lissovsky AA (2009) Diversity of Palaearctic chipmunks (*Tamias*, Sciuridae). Mammalia 73:281–298

Ogino S, Otsuka H, Harunari H (2009) The middle Pleistocene Matsugae fauna, northern Kyushu, West Japan. Paleontol Res 13:367–384

Ohdachi SD, Masuda R, Abe H, Adachi J, Dokuchaev NE, Haukisalmi V, Yoshida MC (1997) Phylogeny of Eurasian soricine shrews (Insectivora, Mammalia) inferred from the mitochondrial cytochrome *b* gene sequences. Zool Sci 14:527–532

Ohdachi SD, Dokuchaev NE, Hasegawa M, Masuda R (2001) Intraspecific phylogeny and geographical variation of six species of northeastern Asiatic *Sorex* shrews based on the mitochondrial cytochrome *b* sequences. Mol Ecol 10:2199–2213

Ohdachi SD, Iwasa MA, Nesterenko VA, Abe H, Masuda R, Haberl W (2004) Molecular phylogenetics of *Crocidura* shrews (Insectivora) in east and central Asia. J Mammal 85:396–403

Ohdachi SD, Hasegawa M, Iwasa MA, Vogel P, Oshida T, Lin L-K, Abe H (2006) Molecular phylogenetics of soricid shrews (Mammalia) based on mitochondrial cytochrome *b* gene sequences: with special reference to the Soricidae. J Zool 270:177–191

Ohdachi SD, Ishibashi Y, Iwasa MA, Fukui D, Saitoh T (2015) The wild mammals of Japan, 2nd edn. Shoukadoh, Kyoto, 506 pp

Ohnishi N, Uno R, Ishibashi Y, Tamate HB, Oi T (2009) The influence of climatic oscillations during the Quaternary era on the genetic structure of Asian black bears in Japan. Heredity 102:579–589

Ohshima K (1991) The late-quaternary sea-level change of the Japanese Islands. J Geogr 100:967–975 (in Japanese)

Okumura H (2004) Complete sequence of mitochondrial DNA control region of the Japanese serow *Capricornis crispus* (Bovidae: Caprinae). Mamm Stud 29:137–145

Okumura N, Ishiguro N, Nakano M, Hirai K, Matsui A, Sahara M (1996) Geographic population structure and sequence divergence in the mitochondrial DNA control region of the Japanese wild boar (*Sus scrofa leucomystax*), with reference to those of domestic pigs. Biochem Genet 34:179–189

Okumura N, Kurosawa Y, Kobayashi E, Watanobe T, Ishiguro N, Yasue H, Mitsuhashi T (2001) Genetic relationship amongst the major non-coding regions of mitochondrial DNAs in wild boars and several breeds of domestic pigs. Anim Genet 32:139–147

Oshida T, Masuda R (2000) Phylogeny and zoogeography of six squirrel species of the genus *Sciurus* (Mammalia, Rodentia), inferred from cytochrome *b* gene sequences. Zool Sci 17:405–409

Oshida T, Masuda R, Yoshida MC (1996) Phylogenetic relationships among Japanese species of the family Sciuridae (Mammalia, Rodentia), inferred from nucleotide sequences of mitochondrial 12S ribosomal RNA genes. Zool Sci 13:615–620

Oshida T, Lin L-K, Masuda R, Yoshida MC (2000a) Phylogenetic relationships among Asian species of *Petaurista* (Rodentia, Sciuridae), inferred from mitochondrial cytochrome *b* gene sequences. Zool Sci 17:123–128

Oshida T, Lin L-K, Yanagawa H, Endo H, Masuda R (2000b) Phylogenetic relationships among six flying squirrel genera, inferred from mitochondrial cytochrome *b* gene sequences. Zool Sci 17:485–489

Oshida T, Ikeda K, Yamada K, Masuda R (2001) Phylogeography of the Japanese giant flying squirrel, *Petaurista leucogenys*, based on mitochondrial DNA control region sequences. Zool Sci 18:107–114

Oshida T, Abramov A, Yanagawa H, Masuda R (2005) Phylogeographjy of the Russian flying squirrel (*Pteromys volans*): implication of refugia theory in arboreal small mammal of Eurasia. Mol Ecol 14:1191–1196

Oshida T, Arslan A, Noda M (2009a) Phylogenetic relationships among the Old World *Sciurus* squirrels. Folia Zool 58:14–25

Oshida T, Masuda R, Ikeda K (2009b) Phylogeography of the Japanese giant flying squirrel, *Petaurista leucogenys* (Rodentia: Sciuridae): implication of glacial refugia in an arboreal small mammal in the Japanese Islands. Biol J Linn Soc 98:47–60

Pagès M, Calvignac S, Klein C, Paris M, Hughes S, Hänni C (2008) Combined analysis of fourteen nuclear genes refines the Ursidae phylogeny. Mol Phylogenet Evol 47:73–83

Park S-C, Yoo D-G, Lee C-W, Lee E-I (2000) Last glacial sea-level changes and paleogeography of the Korea (Tsushima) Strait. Geo-Mar Lett 20:64–71

Perini FA, Russo CAM, Schrago CG (2010) The evolution of South American endemic canids: a history of rapid diversification and morphological parallelism. J Evol Biol 23:311–322

Sakka H, Quere JP, Kartavtseva I, Pavlenko M, Chelomina G, Atopkin D, Bogdanov A, Michaux J (2010) Comparative phylogeography of four *Apodemus* species (Mammalia: Rodentia) in the Asian Far East: evidence of Quaternary climatic changes in their genetic signature. Biol J Linn Soc 100:797–821

Sato JJ (2013) Phylogeographic and feeding ecological effects on the mustelid faunal assemblages in Japan. Anim Syst Evol Divers 29:99–114

Sato JJ (2016) The systematics and taxonomy of the world's badger species: a review. In: Proulx G, Do Linh San E (eds) Badgers of the world: systematics, ecology, behaviour and conservation. Alpha Wildlife, Sherwood Park, pp 1–30

Sato JJ, Suzuki H (2004) Phylogenetic relationships and divergence times of the genus *Tokudaia* within Murinae (Muridae; Rodentia) inferred from the nucleotide sequences encoding for Cyt*b*, RAG1, and IRBP. Can J Zool 82:1343–1351

Sato JJ, Wolsan M (2016) Molecular systematics of the caniform Carnivora and its implications to conservation priority. In: Do Linh San E, Sato JJ, Belant JL, Somers MJ (eds) Small carnivores: evolution, ecology, behaviour and conservation. Wiley Blackwell, Hoboken (in press)

Sato JJ, Hosoda T, Wolsan M, Tsuchiya K, Yamamoto Y, Suzuki H (2003) Phylogenetic relationships and divergence time among mustelids (Mammalia; Carnivora) based on nucleotide sequences of the nuclear interphotoreceptor retinoid binding protein and mitochondrial cytochrome *b* genes. Zool Sci 20:243–264

Sato JJ, Wolsan M, Minami S, Hosoda T, Sinaga MH, Hiyama K, Yamaguchi Y, Suzuki H (2009) Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. Mol Phylogenet Evol 53:907–922

Sato JJ, Hosoda T, Kryukov AP, Kartavtseva IV, Suzuki H (2011) Genetic diversity of the sable (*Martes zibellina*, Mustelidae) in Russian Far East and Hokkaido inferred from mitochondrial NADH dehydrogenase subunit 2 gene sequences. Mamm Study 36:209–222

Sato JJ, Wolsan M, Prevosti FJ, Delia G, Begg C, Begg K, Hosoda T, Campbell KL, Suzuki H (2012) Evolutionary and biogeographic history of weasel-like carnivolans (Musteloidea). Mol Phylogenet Evol 63:745–757

Sato JJ, Ohdachi SD, Echenique-Diaz L, Borroto-Páez L, Begué-Quiala G, Delgado-Labañino JL, Gámez-Díez J, Alvarez-Lemus J, Nguyen ST, Yamaguchi N, Kita M (2016) Molecular phylogenetic analysis of nuclear genes suggests a Cenozoic over-water dispersal origin for the Cuban solenodon. Sci Rep 6:31173

Serizawa K, Suzuki H, Tsuchiya K (2000) A phylogenetic view on species radiation in *Apodemus* inferred from variation of nuclear and mitochondrial genes. Biochem Genet 38:27–40

Serizawa K, Suzuki H, Iwasa MA, Tsuchiya K, Pavlenko MV, Kartavtseva IV, Chelomina GN, Dokuchaev N, Han SH (2002) A spatial aspect on mitochondrial DNA genealogy in *Apodemus peninsulae* from East Asia. Biochem Genet 40:149–161

Shimada T, Aplin K, Jogahara T, Lin K-L, Gonzalez J-P, Herbreteau V, Suzuki H (2007) Complex phylogeographic structuring in a continental small mammal from East Asia, the rice field mouse, *Mus caroli* (Rodentia, Muridae). Mamm Study 32:49–62

Shinohara A, Campbell KL, Suzuki H (2003) Molecular phylogenetic relationships of moles, shrew moles, and desmans from the New and Old Worlds. Mol Phylogenet Evol 27:247–258

Shinohara A, Suzuki H, Tsuchiya K, Zhang YP, Luo J, Jiang X-L, Wang Y-X, Campbell KL (2004) Evolution and biogeography of talpid moles from continental East Asia and the Japanese Islands inferred from mitochondrial and nuclear gene sequences. Zool Sci 21:1177–1185

Shinohara A, Campbell KL, Suzuki H (2005) An evolutionary view on the Japanese talpids based on nuclear sequences. Mamm Study 30:S19–S24

Shinohara A, Kawada S, Son NT, Koshimoto C, Endo H, Can DN, Suzuki H (2014) Molecular phylogeny of East and Southeast Asian fossorial moles (Lipotyphla, Talpidae). J Mammal 95:455–466

Steppan SJ, Adkins RM, Anderson J (2004a) Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Syst Biol 53:533–553

Steppan SJ, Storz BL, Hoffmann RS (2004b) Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. Mol Phylogenet Evol 30:703–719

Steppan SJ, Adkins RM, Spinks PQ, Hale C (2005) Multigene phylogeny of the Old World mice, Murinae, reveals distinct geographic lineages and the declining utility of mitochondrial genes compared to nuclear genes. Mol Phylogenet Evol 37:370–388

Suzuki H (2015) A molecular phylogenetic view of mammals in the “three-story museum” of Hokkaido, Honshu, and Ryukyu Islands, Japan. In: Ohdachi SD, Ishibashi Y, Iwasa MA, Fukui D, Saitoh T (eds) The wild mammals of Japan, second edition. Shoukadoh, Kyoto, pp 269–271

Suzuki H, Iwasa MA, Ishii N, Nagaoka H, Tsuchiya K (1999) The genetic status of two insular populations of the endemic spiny rat *Tokudaia osimensis* (Rodentia, Muridae) of the Ryukyu Islands, Japan. Mamm Study 24:43–50

Suzuki H, Tsuchiya K, Takezaki N (2000) A molecular phylogenetic framework for the Ryukyu endemic rodents *Tokudaia osimensis* and *Diplothrix legata*. Mol Phylogenet Evol 15:15–24

Suzuki H, Sato JJ, Tsuchiya K, Luo J, Zhang Y-P, Wang Y-X, Jiang X-L (2003) Molecular phylogeny of wood mice (*Apodemus*, Muridae) in East Asia. Biol J Linn Soc 80:469–481

Suzuki H, Yasuda SP, Sakaizumi M, Wakana S, Motokawa M, Tsuchiya K (2004) Differential geographic patterns of mitochondrial DNA variation in two sympatric species of Japanese wood mice, *Apodemus speciosus* and *A. argenteus*. Genes Genet Syst 79:165–176

Suzuki H, Filippucci MG, Chelomina GN, Sato JJ, Serizawa K, Nevo E (2008) A biogeographic view of *Apodemus* in Asia and Europe inferred from nuclear and mitochondrial gene sequences. Biochem Genet 46:329–346

Svenning J-C, Fløjgaard C, Marske KA, Nógues-Bravo D, Normand S (2011) Applications of species distribution modeling to paleobiology. Quat Sci Rev 30:2930–2947

Tamada T, Siriaroonrat B, Subramaniam V, Hamachi M, Lin L-K, Oshida T, Rerkamnuaychoke W, Masuda R (2008) Molecular diversity and phylogeography of the Asian leopard cat, *Felis bengalensis*, inferred from mitochondrial and Y-chromosomal DNA sequences. Zool Sci 25:154–163

Tamate HB, Tatsuzawa S, Suda K, Izawa M, Doi T, Sunagawa K, Miyahira F, Tado H (1998) Mitochondrial DNA variations in local populations of the Japanese sika deer, *Cervus nippon*. J Mammal 79:1396–1403

Tashima S, Kaneko Y, Anezaki T, Baba M, Yachimori S, Abramov AV, Saveljev AP, Masuda R (2011) Phylogeographic sympatry and isolation of the Eurasian badgers (*Meles*, Mustelidae, Carnivora): implications for an alternative analysis using maternally as well as paternally inherited genes. Zool Sci 28:293–303

Terashima M, Suyanto A, Tsuchiya K, Moriwaki K, Jin M-L, Suzuki H (2003) Geographic variation of *Mus caroli* from East and Southeast Asia based on mitochondrial cytochrome *b* gene sequences. Mamm Study 28:67–72

Thorington RW Jr, Hoffmann RS (2005) Family Sciuridae. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 754–818

Tomozawa M, Suzuki H (2008) A trend of central versus peripheral structuring in mitochondrial and nuclear gene sequences of the Japanese wood mouse, *Apodemus speciosus*. Zool Sci 25:273–285

Tosi AJ, Morales JC, Melnick DJ (2003) Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. Evolution 57:1419–1435

Tsuchiya K, Suzuki H, Shinohara A, Harada M, Wakana S, Sakaizumi M, Han S-H, Lin L-K, Kryukov A (2000) Molecular phylogeny of East Asian moles inferred from the sequence variation of the mitochondrial cytochrome *b* gene. Genes Genet Syst 75:17–24

Vigilant L, Pennington R, Harpending H, Kocher TD, Wilson AC (1989) Mitochondrial DNA sequences in single hairs from a southern African population. Proc Natl Acad Sci USA 86:9350–9354

Warren BH, Simberloff D, Ricklefs RE, Aguilée R, Condamine FL, Gravel D, Morlon H, Mouquet N, Rosindell J, Casquet J, Conti E, Cornuault J, Fernández-Palacios JM, Hengl T, Norder SJ, Rijsdijk KF, Sanmartín I, Strasberg D, Triantis KA, Valente LM, Whittaker RJ, Gillespie RG, Emerson BC, Thébaud C (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecol Lett 18:200–217

Watanobe T, Okumura N, Ishiguro N, Nakano M, Matsui A, Sahara M, Komatsu M (1999) Genetic relationship and distribution of the Japanese wild boar (*Sus scrofa leucomystax*) and Ryukyu wild boar (*Sus scrofa riukiuanus*) analysed by mitochondrial DNA. Mol Ecol 8:1509–1512

Watanobe T, Ishiguro N, Nakano M (2003) Phylogeography and population structure of the Japanese wild boar *Sus scrofa leucomystax*: mitochondrial DNA variation. Zool Sci 20:1477–1489

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annu Rev Ecol Syst 33:475–505

Werdelin L, Wesley-Hunt GD (2010) The biogeography of carnivore ecomorphology. In: Goswami A, Friscia A (eds) Carnivoran evolution: new views on phylogeny, form, and function. Cambridge University Press, Cambridge, pp 225–245

Wozencraft WC (2005) Order Carnivora. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins Univercity Press, Baltimore, pp 532–628

Wu C, Wu J, Bunch TD, Li Q, Wang Y, Zhang Y-P (2005) Molecular phylogenetics and biogeography of *Lepus* in eastern Asia based on mitochondrial DNA sequences. Mol Phylogenet Evol 37:45–61

Yamada F, Takaki M, Suzuki H (2002) Molecular phylogeny of Japanese Leporidae, the Amami rabbit *Pentalagus furnessi*, the Japanese hare *Lapus brachyurus*, and the mountain hare *Lepus timidus*, inferred from mitochondrial DNA sequences. Genes Genet Syst 77:107–116

Yasuda SP, Vogel P, Tsuchiya K, Han S-H, Lin L-K, Suzuki H (2005) Phylogeographic patterning of mtDNA in the widely distributed harvest mouse *Micromys minutus* suggests dramatic cycles of range contraction and expansion during the mid- to late Pleistocene. Can J Zool 83:1411–1420

Yasuda SP, Minato S, Tsuchiya K, Suzuki H (2007) Onset of cryptic vicariance in the Japanese dormouse *Glirulus japonicus* (Mammalia, Rodentia) in the Late Tertiary, inferred from mitochondrial and nuclear DNA analysis. J Zool Syst Evol Res 45:155–162

Yasuda SP, Iwabuchi M, Aiba H, Minato S, Mitsuishi K, Tsuchiya K, Suzuki H (2012) Spatial framework of nine distinct local populations of the Japanese dormouse *Glirulus japonicus* based on matrilineal cytochrome *b* and patrilineal SRY gene sequences. Zool Sci 29:111–120

Yasukochi Y, Nishida S, Han S-H, Kurosaki K, Yoneda M, Koike H (2009) Genetic structure of the Asiatic black bear in Japan using mitochondrial DNA analysis. J Hered 100:297–308

Yu N, Zheng C, Zhang Y-P, Li W-H (2004) Molecular systematics of pikas (genus *Ochotona*) inferred from mitochondrial DNA sequences. Mol Phylogenet Evol 16:85–95

Yu L, Li Y-W, Ryder OA, Zhang Y-P (2007) Analysis of complete mitochondrial genome sequences increases phylogenetic resolution of bears (Ursidae), a mammalian family that experienced rapid speciation. BMC Evol Biol 7:198

Yuan S-L, Jiang X-L, Li Z-J, He K, Harada M, Oshida T, Lin L-K (2013) A mitochondrial phylogeny and biogeographical scenario for Asiatic water shrews of the genus *Chimarrogale*: implications for taxonomy and low-latitude migration routes. PLoS One 8:e77156

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693

Zemlemrova ED, Bannikova AA, Abramov AV, Lebedev VS, Rozhnov VV (2013) New data on molecular phylogeny of the East Asian moles. Dokl Biol Sci 451:257–451

Chapter 4
Biogeographic Pattern of Japanese Birds: A Cluster Analysis of Faunal Similarity and a Review of Phylogenetic Evidence

Takeshi Yamasaki

Abstract The Japanese islands accommodate 102 native breeding species/subspecies of water birds (comprising 99 species belonging to 58 genera and 22 families) and 246 native breeding species/subspecies of land birds (comprising 156 species belonging to 101 genera and 40 families). The degree of endemism at the species/subspecies level is low in the former (11.8 %) and high in the latter (47.2 %). In this chapter, I investigated the geographic patterns of the community composition of land birds in detail. Using hierarchical and nonhierarchical methods, the cluster analysis of faunal similarity revealed that, despite high vagility, land birds on continental islands exhibited the same biogeographic patterns as other terrestrial vertebrates. This result suggests that the land birds and non-volant terrestrial vertebrates have evolved under the strong influence of the island geohistory, including the appearance and disappearance of land bridges. The cluster analysis also revealed that, in contrast to the non-volant terrestrial vertebrates, the Japanese land birds formed comparatively rich and distinct faunas on these oceanic islands.

Keywords Japanese birds • Species diversity • Endemism • Biogeography • Continental islands • Oceanic islands • Cluster analysis • Faunal similarity

4.1 Introduction

4.1.1 History of Studies on Japanese Avifauna

Japan is a long chain of islands located off the eastern coast of continental China (Fig. 4.1). It comprises four main islands, Hokkaido, Honshu, Shikoku, and Kyushu, with more than 6800 adjacent islands (Statistics Bureau, Ministry of Internal Affairs and Communications 2015). These islands differ greatly in geological and

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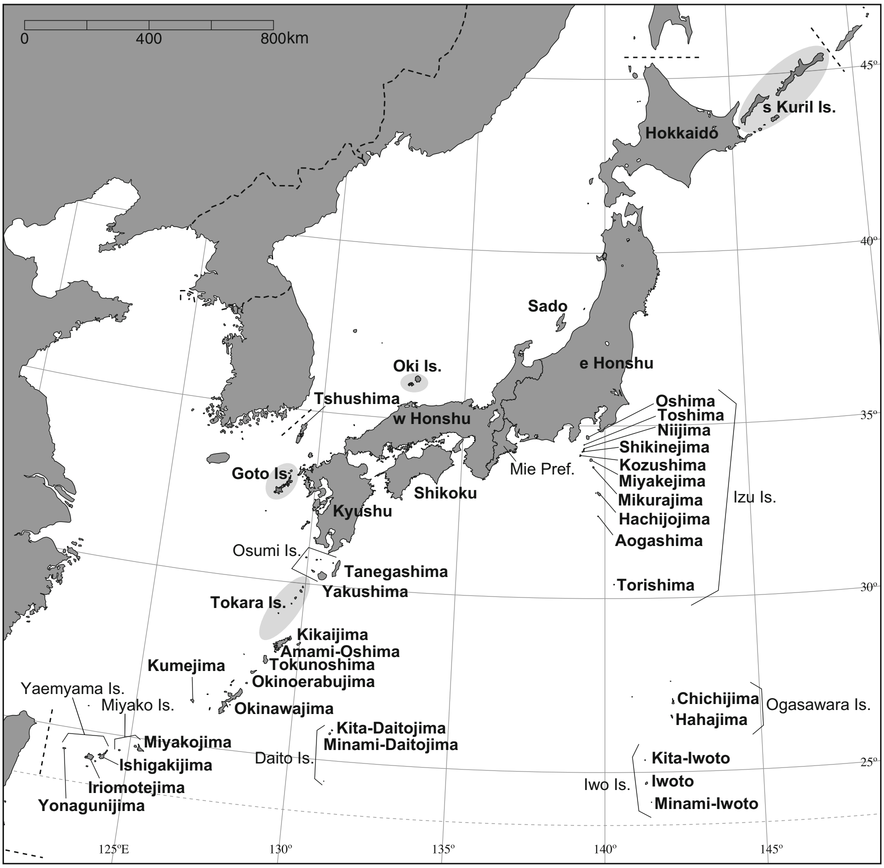

Fig. 4.1 Map of Japan showing location of the 40 study sites (in *bold letters*)

environmental traits (e.g., area, altitude, geological origin, climate, and vegetation) and thus support a rich avifauna.

Although scientific research on Japanese birds had already begun in the late eighteenth century, at that time, Japan was officially closed to all Western nations, except The Netherlands. Thus, because of the paucity of collection material, research activity was low (Dekker et al. 2001; Morioka et al. 2005). Since then, studies on the diversity of Japanese birds have gone through three major periods of high activity (Fig. 4.2).

The first peak was in the 1830s to the 1840s. During this period, the famous series *Fauna Japonica* was published, in which Coenraad Jacob Temminck, the director of the National Museum of Natural History in Leiden, and Hermann Schlegel, a curator of vertebrates, described about 50 new species or subspecies. They examined the large collection of Franz Philipp Balthasar von Siebold, a German naturalist who resided in Japan in the 1820s as a medical officer of the Dutch trading post (Mearns and Mearns 1988; Morioka et al. 2005). Additionally,

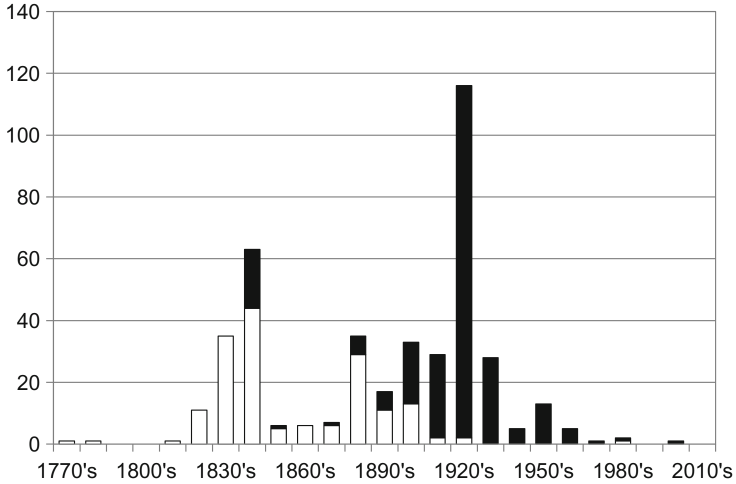

Fig. 4.2 Temporal trends in the number of newly described species/subspecies of Japanese birds. Taxa now in synonymy are included, but those based on fossils or subfossils are excluded. (Data are derived from Morioka et al. 2005). A subspecies described in 2009 (Nishiumi and Morioka 2009) is also included. *White bars* indicate species. *Black bars* indicate subspecies

during this period, Nicholas Aylward Vigor, an Irish naturalist, and Friedrich Heinrich von Kittlitz, a German naturalist, described about 10 new species or subspecies from the Ogasawara Islands, which were then claimed as a British territory (Mearns and Mearns 1988; Morioka et al. 2005).

In the 1860s, Japan was opened to the Western world. However, research activity did not increase, likely because of a sharp decline in public safety (Fig. 4.2). The second peak of new bird descriptions appeared in the 1880s, when public order was restored. During this period, Leonhard Hess Stejneger, a curator of the U.S. National Museum, and Henry Seebohm, an English ornithologist, described 30 or so new species/subspecies using many of the specimens gathered by Thomas Wright Blakiston, Henry James Stovin Pryer, Motoyoshi Namiye, and others (see the American Ornithologists' Union 1919; Mearns and Mearns 1988; Morioka et al. 2005).

In the decades after the second peak, species-level descriptions declined substantially, whereas reports of new subspecies increased considerably. The third major period of new bird descriptions took place in the 1920s. This, the most prominent peak, was mainly attributable to works by two Japanese ornithologists, Nagamichi Kuroda and Tokutaro Momiyama. However, most of the scientific names proposed by the latter (91.1 %) are now regarded as junior synonyms of other bird names, whereas many of the birds described by the former are considered valid (Kuroda 1932; Vaurie 1959, 1965; Morioka 1979; Morioka et al. 2005).

Since the third peak period, the rate of new bird descriptions has declined. In the past 70 years, despite the gross increase of ornithological studies in Japan (Fig. 4.3), only 24 new species or subspecies have been reported from Japan (in contrast to

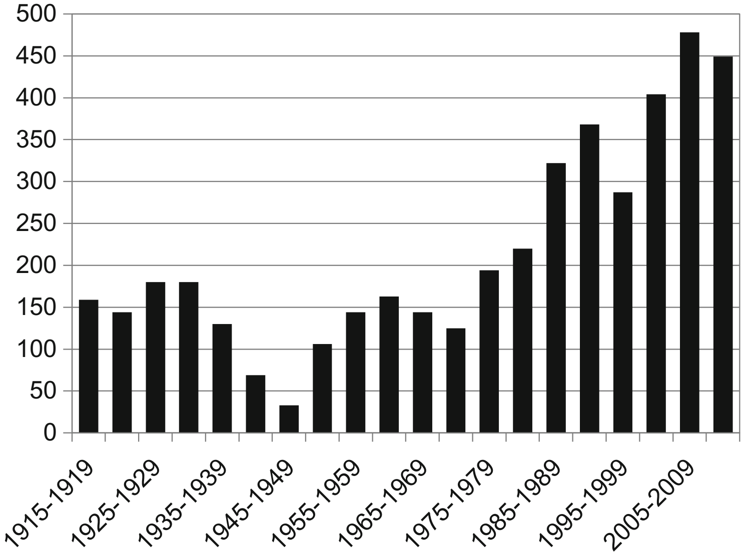

Fig. 4.3 Temporal trends in the number of articles published in Japanese ornithological journals. Total numbers of articles in the following seven journals are shown every 5 years: Tori, Japanese Journal of Ornithology, Ornithological Science, Journal of the Yamashina Institute for Ornithology, Strix, the Bulletin of the Japanese Bird Banding Association and Bird Research. Data were gathered from the J-STAGE database (https://www.jstage.jst.go.jp/browse) and three journals' home pages (http://www.wbsj.org/activity/conservation/publications/strix/, http://birdbanding-assn.jp/J03_bulletin/archive.html, http://www.bird-research.jp/1_kenkyu/index.html)

265 in the preceding seven decades), no fewer than 18 of which are now regarded as invalid (Morioka et al. 2005; Nishiumi and Morioka 2009). This situation clearly means that the possibility of finding new species and subspecies of Japanese birds has become vanishingly small. Instead, during the past seven decades, research on Japanese avifauna has mainly focused on taxonomic revisions of subspecies previously proposed based on insufficient evidence (e.g., Vaurie 1959, 1965; Morioka 1994; Yamasaki 2006). In particular, many subspecies based on arbitrary division of clinal variation have been invalidated. As a result, our understanding of geographic patterns of phenotypic variations of Japanese birds has become considerably more robust. In addition, during this period, details of the geographic distributions, including records of rare vagrants, have also been studied vigorously. Therefore, despite a few new bird descriptions, the number of species recorded in Japan has increased steadily (for example, 489, 542, and 633 native species reported by the Ornithological Society of Japan 1974, 2000, and 2012, respectively).

Now that considerable relevant information has been gathered, it is an appropriate time to discuss the characteristics and formation processes of the Japanese avifauna.

4.1.2 Comparison of the Avifaunas of Japan and the British Isles

Japan and the British Isles are similar island groups of comparable sizes (see Table 4.1), equally situated on the periphery of the Eurasian continent. Based on this information, Hachisuka (1925) attempted to compare the avifaunas of Japan and the British Isles to illustrate the characteristics of each fauna. However, he eventually only gathered relevant information and avoided deriving conclusions, because he believed that the information available to him was still very incomplete. Ninety years have passed, and I conducted a similar comparison using materials accumulated since Hachisuka's work.

The results of the comparison are summarised in Tables 4.1 and 4.2, which show that Japan has 255 native breeding species belonging to 159 genera, 62 families, and 20 orders, whereas the British Isles have 205 species belonging to 131 genera, 58 families, and 20 orders. It is noteworthy that the number of species per unit area (species density) is larger in Japan than in the British Isles: this is also true for both the water bird subgroup (defined here as birds belonging to Anseriformes, Podicipediformes, Phaethontiformes, Gaviiformes, Procellariiformes, Ciconiiformes, Suliformes, Pelecaniformes, Gruiformes, and Charadriiformes) and the land bird subgroup (defined here as birds belonging to Galliformes, Columbiformes, Cuculiformes, Caprimulgiformes, Apodiformes, Accipitriformes, Strigiformes, Coraciiformes, Piciformes, Falconiformes, and Passeriformes). Moreover, the results also reveal that the Japanese land birds encompass more pronounced intraspecific geographic variation than those of the British Isles, although the degree of geographic variation is almost the same in water birds, which include most highly vagile species (e.g., pelagic birds). These patterns seem to reflect the more heterogeneous climates of Japan resulting from the elongated shape of the land from north to south (Fig. 4.1) and mountainous terrain (Table 4.1). However, Table 4.2 also shows that, in contrast to the general patterns, the British Isles have more breeding species than Japan in three orders (Anseriformes, Gaviiformes, and Charadriiformes). This pattern seems to be present mainly

Table 4.1 Comparisons of geographic traits of Japan and the British Isles

	Japan	The British Isles
Area (km^2)[a]	364,560	311,580
Forest cover (%)[a]	68.6	11.7
The latitude of the northernmost point[b]	45.55°N	60.86°N
The latitude of the southernmost point[b]	20.42°N	48.95°N
The highest peak (m)[c]	3,776	1,343

[a] Values for 2012 are shown. Water bodies are excluded. Data were extracted from The World Bank (2015)

[b] Data were gathered using Google Maps (https://maps.google.com)

[c] Data were extracted from Statistics Bureau, Ministry of Internal Affairs and Communications (2015) (for Japan) and Merriam-Webster (1997) (for the British Isles)

Table 4.2 Comparisons of native breeding avifaunas of Japan and the British Isles

	Japan					The British Isles				
Order	Family	Genus	Species[a]	Species/ subspecies	Sub-speciation[b]	Family	Genus	Species[a]	Species/ subspecies	Sub-speciation[b]
Water birds										
Anseriformes	1	8	14(0.38)	14	1.00	1	9	17(0.55)	17	1.00
Podicipediformes	1	2	3(0.08)	4	1.33	1	2	4(0.13)	4	1.00
Phaethontiformes	1	1	1(0.03)	1	1.00	0	0	0(0.00)	0	
Gaviiformes	0	0	0(0.00)	0		1	1	2(0.06)	2	1.00
Procellariiformes	3	6	14(0.38)	14	1.00	2	4	4(0.13)	4	1.00
Ciconiiformes	1	1	1(0.03)	1	1.00	1	1	1(0.03)	1	1.00
Suliformes	3	3	7(0.19)	7	1.00	2	2	3(0.10)	4	1.33
Pelecaniformes	2	9	17(0.47)	17	1.00	2	4	4(0.13)	4	1.00
Gruiformes	2	8	10(0.27)	11	1.10	3	7	8(0.26)	8	1.00
Charadriiformes	8	20	32(0.88)	33	1.03	8	26	40(1.28)	43	1.08
Subtotal	22	58	99(2.72)	102	1.03	21	56	83(2.66)	87	1.05
Land birds										
Galliformes	1	5	5(0.14)	12	2.40	1	4	6(0.19)	6	1.00
Columbiformes	1	4	7(0.19)	11	1.57	1	2	5(0.16)	5	1.00
Cuculiformes	1	2	4(0.11)	4	1.00	1	1	1(0.03)	1	1.00
Caprimulgiformes	1	1	1(0.03)	1	1.00	1	1	1(0.03)	1	1.00
Apodiformes	1	2	3(0.08)	4	1.33	1	1	1(0.03)	1	1.00
Accipitriformes	2	11	13(0.36)	16	1.23	2	8	11(0.35)	11	1.00
Strigiformes	1	7	9(0.25)	15	1.67	2	4	5(0.16)	5	1.00
Coraciiformes	2	4	4(0.11)	6	1.50	1	1	1(0.03)	1	1.00
Piciformes	1	6	11(0.30)	25	2.27	1	3	4(0.13)	4	1.00
Falconiformes	1	1	3(0.08)	4	1.33	1	1	4(0.13)	4	1.00
Passeriformes	28	58	96(2.63)	148	1.54	25	49	83(2.66)	100	1.20

Subtotal	40	101	156(4.28)	246	1.58	37	75	122(3.92)	139	1.14
Total	62	159	255(6.99)	348	1.36	58	131	205(6.58)	226	1.10

Ordinal and familiar taxonomy follows The Ornithological Society of Japan (2012). Generic, specific and subspecific taxonomy and distributional data were based on The Ornithological Society of Japan (2012) (for Japan) and Parkin and Knox (2010) (for the British Isles)

[a] Values in parentheses represent species density (the number of species per 10^4 km^2)

[b] The total number of species/subspecies is divided by the total number of species to reflect the intensity of intraspecific geographic variation

because these orders of the British Isles include many migratory species preferring water bodies at high latitudes (Gooders 1982). The British Isles, which are located at a more northern latitude than the Japanese islands (Table 4.1), abound in such environments.

Additionally, compared with the British Isles, Japan also has more forest-dwelling birds and fewer open-habitat birds. For example, 72.9 % (113/155) of Japanese breeding land bird species are observed in some sort of woodland in the breeding season, whereas only 49.2 % (60/122) exploit woodlands in the British Isles [calculated based on habitat information provided by the Ornithological Society of Japan (2012) and Nakamura and Nakamura (1995) for Japanese birds, and by Gooders (1982) and del Hoyo et al. (2010) for those of the British Isles]. This pattern may reflect the fact that much higher forest cover is observed in the Japanese islands (Table 4.1).

4.1.3 A Comparison of Fauna of Japanese Birds and Other Terrestrial Vertebrates

As well as birds, the other terrestrial vertebrate faunas of Japan are also characterised by the high species richness (Sengoku et al. 1996; Abe et al. 2005); interestingly, detailed inspection reveals a markedly different pattern of diversity among them. In particular, although the Japanese native avifauna (633 species including 255 regularly breeding birds) is much richer than that of mammals, reptiles, and amphibians (110, 66, and 59 species, respectively, excluding marine species), their degree of endemism is much lower. Only 7.1 % of the breeding birds (14 resident and 4 migratory species; Table 4.3) are endemic to Japan, whereas no less than 40.0 % of mammals, 56.1 % of reptiles, and 78.0 % of amphibians are endemic (Sengoku et al. 1996; Abe et al. 2005; The Ornithological Society of Japan 2012).

In a series of biogeographic studies, Morioka argued that the paucity of endemism in Japanese birds is attributable to recent colonisation by continental birds across sea barriers and subsequent replacement of native species (Morioka 1971, 1974; Morioka and Sakane 1980). He considered that geohistorical factors, for example, sea level changes during the glacial periods, had little influence on the distribution of Japanese birds, although they are often considered the most significant factors for the evolution of Japan's mammalian fauna and herpetofauna (Ota 1998, 2000; Millien-Parra and Jaeger 1999).

Morioka's studies, similar to those of other contemporary researchers (e.g., Short 1973), did not use numerical and objective comparative methods. Furthermore, since his studies were published, substantial taxonomic changes have taken place (e.g., Yamasaki 2006; Saitoh et al. 2010) and new information on distribution has been published (see Sect. 4.1.1). In the following sections, I conduct a numerical cluster analysis of local assemblages of Japanese breeding birds using recently

Table 4.3 Bird species endemic to Japan

Species	Common name	Resident/ migratory	Family
Water birds[a]			
Gorsachius goisagi[b]	Japanese Night Heron	Migratory	Ardeidae
Gallirallus okinawae	Okinawa Rail	Resident	Rallidae
Scolopax mira	Amami Woodcock	Resident	Scolopacidae
Land birds[c]			
Syrmaticus soemmerringii	Copper Pheasant	Resident	Phasianidae
Columba versicolor	Bonin Wood Pigeon	Resident	Columbidae
Columba jouyi	Ryukyu Wood Pigeon	Resident	Columbidae
Picus awokera	Japanese Green Woodpecker	Resident	Picidae
Sapheopipo noguchii	Okinawa Woodpecker	Resident	Picidae
Garrulus lidthi	Lidth's Jay	Resident	Corvidae
Phylloscopus xanthodryas	Japanese Leaf Warbler	Migratory	Phylloscopidae
Phylloscopus ijimae	Ijima's Leaf Warbler	Migratory	Phylloscopidae
Apalopteron familiare	Bonin White-eye	Resident	Zosteropidae
Cichlopasser terrestris	Bonin Thrush	Resident	Muscicapidae
Turdus celaenops	Izu Thrush	Resident	Muscicapidae
Luscinia komadori	Ryukyu Robin	Resident	Muscicapidae
Prunella rubida	Japanese Accentor	Resident	Prunellidae
Chaunoproctus ferreorostris	Bonin Grosbeak	Resident	Fringillidae
Emberiza sulphurata	Yellow Bunting	Migratory	Emberizidae

This table includes species whose breeding distributions are confined to (but winter outside of) Japanese territory. Data were obtained from The Ornithological Society of Japan (2012)

[a] Breeding ranges of Bryan's Shearwater *Puffinus bryani* Pyle, Welch and Fleischer, 2011 are not well known. Future studies might show that it is a breeding bird endemic to Japan

[b] There are a few records of casual breeding of this species in Taiwan and Korea (BirdLife International 2015)

[c] OSJ (2012) considered the Japanese Wagtail, *Motacilla grandis*, to be a casual breeder in Korea, where this species may actually be a rare but locally abundant resident bird (Choi and Nam 2008)

published material. The purpose of this study is to elucidate the geographic patterns of faunal similarities among local assemblages and to identify factors that significantly influenced the Japanese avifauna formation.

4.2 Materials and Methods

I selected 35 islands and four island groups that have been comparatively well surveyed and cover almost the entire range of Japan as independent units for the analysis (Fig. 4.1). Morioka and Sakane (1980) pointed out that the largest island, Honshu, has two considerably different avifaunas in its northeastern and southwestern regions. Thus, I treated these two regions as separate units for the following analyses. The northeastern avifauna includes birds from Niigata, Nagano, Gifu, and Aichi Prefectures and eastward. The southwestern avifauna includes Toyama, Ishikawa, Fukui, Shiga, Kyoto, Nara, and Wakayama Prefectures and westward. Birds from Mie Prefecture were ignored, because this area has a mixture of the two aforementioned faunas. As for the four island groups (southern Kuril, Oki, Goto, and Tokara Islands), it was difficult to treat each island as an independent unit because of the lack of detailed distribution information. For each of the 40 localities examined, I compiled a list of native species/subspecies that breed there regularly. I also recorded whether each taxon is endemic to the Japanese territory. Taxonomic and distributional data were obtained from The Ornithological Society of Japan (2012).

To describe the geographic pattern of faunal similarity within Japan, I computed the Simpson's similarity indices (S) for all pairwise comparisons among the 40 local communities at both the species and species/subspecies levels. The formula $S = C/N$ was used, where C is the number of shared species or species/subspecies, and N the number of species or species/subspecies in the smaller community. The calculations were done using data on land birds only. The values were then converted into distances (D) by the formula: $D = 1 - S$. The resulting distance matrices were subjected to cluster analysis using the unweighted pair-group means algorithm (UPGMA). For computation and visualisation of results, I used two computer programs, PHYLIP version 3.695 (Felsenstein 1989) and MEGA version 6.06 (Tamura et al. 2013). To assess the degree of support for each of the UPGMA clusters, I also conducted bootstrap analysis using the macro language VBA with the RANDBETWEEN and INDEX functions in Excel® 2010 (Microsoft, Redmond, WA, USA). Random selection of species or species/subspecies was carried out 1000 times. Bootstrap replicates, including zero-sized communities, made it impossible to calculate D; they were therefore discarded and a recalculation was done.

To evaluate possible biases arising from the lack of phylogenetic information (Holt et al. 2013), I conducted a preliminary UPGMA cluster analysis incorporating available, albeit incomplete, phylogenetic information. For this purpose, I used the method recently developed by Holt et al. (2013). This preliminary analysis was only done for the species/subspecies level. I assumed that each order, family, genus, and species in the classification of The Ornithological Society of Japan (2012) represented a monophyletic group. I also postulated polytomies at the ordinal, familiar, generic, specific, and subspecific levels. Using the resulting phylogenetic relationship, I calculated the modified Simpson's indices following the formula $S' = C'/N'$, where C' is the number of shared phylogenetic branches, and N' the number of branches in the smaller community. These data were then analysed as already described.

As a complementary nonhierarchical description of the geographic pattern of faunal similarity, I also plotted the 40 local communities in three-dimensional space based on the multidimensional scaling (MDS) procedure with the ordinal level option in SAS version 9.3 (SAS, Cary, NC, USA). For this analysis, I used the aforementioned D distance matrix calculated at the species/subspecies level without incorporating phylogenetic information.

4.3 Results

The native fauna of regularly breeding birds in Japan includes 99 species (38.8 %) of water birds and 156 species (61.2 %) of land birds (Table 4.4). Compared with the mammalian fauna and herpetofauna, the percentages of endemic species are much smaller in both water birds (3.0 %) and land birds (9.6 %). The degree of endemism in the water birds is low even at the species/subspecies level (11.8 %). However, as with the land birds, a considerably large fraction of species/subspecies are confined to the Japanese territory (47.2 %) (Table 4.4).

At the species level, the UPGMA dendrogram of land bird faunal similarity yielded only two small clusters with high bootstrap supports (>70 %): one combining Hokkaido and the southern Kuril Islands (bootstrap value = 76 %) and the other combining Yakushima and Tanegashima (bootstrap value = 87 %). In contrast, the UPGMA dendrogram based on data at the species/subspecies level detected no less than 15 distinct clusters with high bootstrap support (Fig. 4.4). The preliminary UPGMA dendrogram incorporating phylogenetic information also supported, or at least did not refute, the presence of these 15 clusters (Fig. 4.5). There were 5 main clusters: (1) the four main islands of Japan together with some adjacent islands, or the Japanese Archipelago, and the Izu Islands, (2) Yakushima and Tanegashima, (3) the Daito Islands, (4) the central and southern Ryukyus, and (5) the Ogasawara and Iwo Islands. The Tokara Islands are not included in any of these clusters at the top level. In the first cluster (1), the first node isolates (6) Hokkaido and the southern Kuril Islands from (7) the other localities. The second node separates (9) the Izu Islands and (8) the others. Cluster 8 contains a well-supported subcluster, (10) eastern Honshu and Sado. Cluster 4 is divided into the (11) central and (12) southern Ryukyus. The latter is further divided into the Miyako and (13) Yaeyama Islands. The highest level cluster 5 consists of two well-supported subclusters, (14) Ogasawara and (15) the Iwo Islands.

The multidimensional scaling analysis scatterplot (Fig. 4.6) supported the presence of 14 of the 15 clusters described. However, it did not confirm the close relationship between eastern Honshu and Sado.

Table 4.4 Summary of the native breeding avifauna of Japan

	Species		Species/subspecies	
	Total	Endemic[a]	Total	Endemic[a]
Water birds	99	3 (3.0 %)	102	12 (11.8 %)
Land birds	156	15 (9.6 %)	246	116 (47.2 %)
Total	255	18 (7.1 %)	348	128 (36.8 %)

[a] Birds whose breeding distributions are confined to Japanese territory

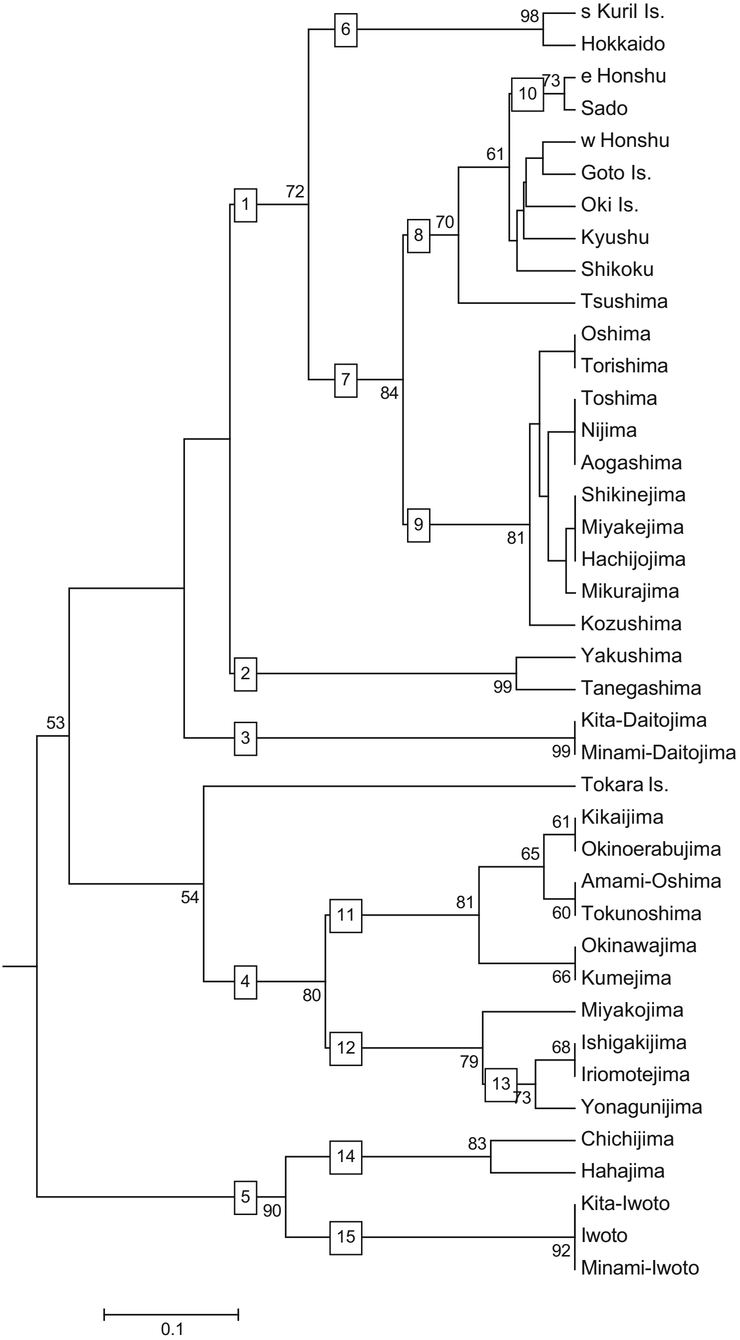

Fig. 4.4 Unweighted pair-group means algorithm dendrogram of faunal similarity for the native breeding land birds of Japan based on Simpson's similarity indices calculated at the species/subspecies level. Bootstrap values >50 % are shown at the nodes. Highly supported clusters (>70 %) are numbered serially

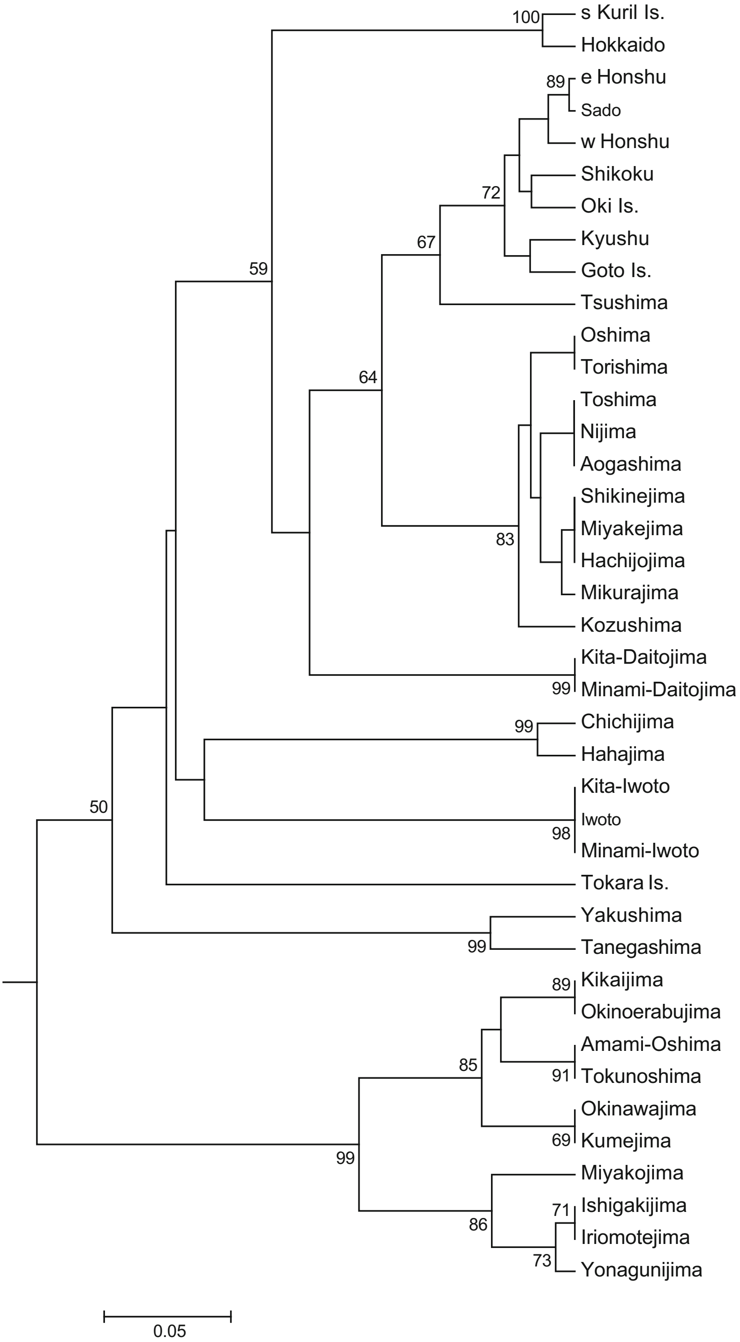

Fig. 4.5 Unweighted pair-group means algorithm dendrogram of faunal similarity for the native breeding land birds of Japan based on corrected Simpson's similarity indices calculated at the species/subspecies level incorporating phylogenetic information. Bootstrap values >50 % are shown at the nodes

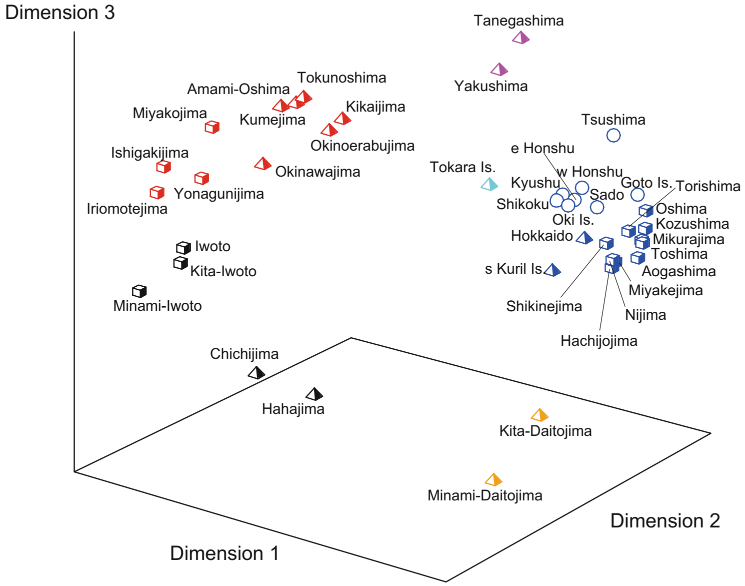

Fig. 4.6 Scatterplot of the multidimensional scaling analysis for faunal similarity of the native breeding land birds based on Simpson's similarity indices calculated at the species/subspecies level. Different colours show different major clusters of the UPGMA analysis (see Fig. 4.4). Tokara Islands, which do not belong to any of the top-level clusters, are represented by *cyan*. Different *marks* indicate different subclusters

4.4 Discussion

The Japanese avifauna does not exhibit either high endemism or any strong biogeographic structure at the species level (see Table 4.4 and Sect. 4.3). These results appear to support Morioka's hypothesis that the Japanese avifauna would have been formed through recent colonisation by continental birds across sea barriers and the subsequent rapid replacement of native species (Morioka 1971, 1974; Morioka and Sakane 1980). He also postulated that geohistorical factors, such as sea level changes during the glacial periods, had little influence on the distribution of Japanese birds.

However, the present study also revealed that, aside from water birds, which include birds that have a very wide distribution range (e.g., pelagic birds), the Japanese birds exhibit a considerably high degree of endemism at the specific/subspecific level (see Table 4.4). Morioka considered these subspecies as only slightly different from their continental counterparts in terms of phenotypic characteristics, and thus concluded that they have not been geographically isolated for long (Morioka and Sakane 1980). He argued that biogeographic analyses of Japanese birds should not be carried out on subspecific-level data (Morioka 1971). However, diagnostic traits possessed by Japanese endemic subspecies, even if they seem trivial, are potential evidence that these subspecies have a biogeographic history independent from continental birds (Cracraft 1983). Moreover, in contrast to Morioka's view of close affinity, a recently published analysis of DNA barcode data reported that several of these subspecies are actually highly genetically divergent from other conspecifics; of 156 land birds breeding in Japan, at least 24 species have intraspecific variation greater than 1.6 % Kimura two-parameter distance (Saitoh et al. 2015), which is a distance threshold proposed for delimiting bird species of the Eurasian continent (Kerr et al. 2009). To date, only a fraction of the 24 species have been studied in detail, but the presence of many cryptic endemic species has already been confirmed (Saitoh et al. 2010; McKay et al. 2014; Dong et al. 2015). Thus, it seems likely that the frequency of bird species endemic to Japan will increase with further research.

The high degree of endemism of the Japanese land birds at the specific/subspecific level seems to suggest that sea straits separating the Japanese islands and continental China have served as important biogeographic barriers, even for these highly vagile animals. The faunal similarity analysis conducted at the species/subspecies level also indicated the possibility that, as with terrestrial vertebrates, the Japanese land bird fauna has evolved under the strong influence of geohistory. The analysis revealed the presence of the same biogeographic regions as those found in surveys on non-volant terrestrial vertebrates (Fig. 4.4) (Ota 1998, 2000; Millien-Parra and Jaeger 1999).

Excluding the oceanic islands, the Japanese islands are grouped into two main regions, the Japanese Archipelago and the Ryukyu Archipelago; in the Japanese Archipelago, the Tsugaru Strait separating Hokkaido and Honshu serves as a biogeographic border; despite low bootstrap support, the Tsushima Strait, located between Tsushima and Kyushu, might also be another biogeographic border (see also Figs. 4.5 and 4.6). The Ryukyu Archipelago is further divided into two subregions, the central and southern Ryukyus. It is noteworthy that each of these regions and subregions has many endemic species/subspecies (Table 4.5). These species/subspecies have either evolved in situ or only survived in one place, suggesting that each of the regions/subregions has a distinct evolutionary history.

The multidimensional scaling analysis of faunal similarity (Fig. 4.6) revealed that the avifaunas of Yakushima, Tanegashima, and the Tokara Islands have characteristics intermediate of those in the Japanese and Ryukyu archipelagos. However, the Yakushima and Tanegashima avifauna is not a simple mix but is characterised as having comparatively many endemic species/subspecies (Table 4.5). The Osumi Islands, which comprise Yakushima and Tanegashima together with adjacent islets, exhibit very high environmental heterogeneity, such as high mountain ranges (~2000 m) and plains, which might promote strong divergent natural selection, the driving force of the ecological speciation process. In contrast to this, no endemic birds are known from the Tokara Islands, although some authors suggest the possibility of undescribed forms (Morioka 1990; Seki et al. 2011). A study on the herpetofauna of this area revealed the presence of a biogeographic border at the strait within the islands (Ota 1998, 2000). For birds, it is

Table 4.5 Summary of native land birds breeding in each of Japan's 17 biogeographic regions

Region	Species/subspecies	
	Total	Endemic[a]
1. The Japanese archipelago (including the Izu Islands)	182	49 (26.9 %)
2. Yakushima and Tanegashima	32	5 (15.6 %)
3. Daito Islands	13	6 (46.2 %)
Tokara Islands	25	0 (0.0 %)
4. Central and southern Ryukyus	51	25 (49.0 %)
5. Ogasawara and Iwo Islands	17	13 (76.5 %)
6. Hokkaido and the southern Kuril Islands	120	6 (5.0 %)
7. Honshu, Shikoku, and Kyushu with adjacent islands and Izu Islands	149	35 (23.5 %)
8. Honshu, Shikoku, and Kyushu with adjacent islands	141	28 (19.9 %)
9. Izu Islands	39	4 (10.3 %)
10. Eastern Honshu and Sado	123	9 (7.3 %)
11. Central Ryukyus	38	9 (23.7 %)
12. Southern Ryukyus	29	11 (37.9 %)
Miyako Islands	17	0 (0.0 %)[b]
13. Yaeyama Islands	27	8 (29.6 %)
14. Ogasawara Islands	14	7 (50.0 %)
15. Iwo Islands	8	3 (37.5 %)

The numbers before the region names refer to the cluster number in the unweighted pair-group means algorithm dendrogram (see Fig. 4.4)

[a] Birds whose breeding distributions are confined to the biogeographic region

[b] Miyako Island Kingfisher, *Todiramphus miyakoensis*, which is known by a single specimen from Miyakojima Island, was excluded from the analysis because it is possible that it does not breed there (Morioka 1974)

difficult to perform analysis using each island as a unit of comparison because of the paucity of information on the distribution of birds breeding within the islands.

The only obvious difference in biogeographic patterns between the land birds and other terrestrial vertebrates is that biogeographic regions comprising oceanic islands are only seen in the former. The oceanic islands Izu, Daito, Ogasawara, and Iwo have comparatively rich and distinct avifaunas (Fig. 4.4, Table 4.5), but they have poor non-volant terrestrial vertebrate faunas. Highly vagile land birds seem to have been able to colonise these isolated islands and experienced rapid evolution in the face of strong natural selection attributable to the poor biotas.

4.5 Conclusion

In summary, the land birds breeding in Japan exhibit a high degree of endemism at the specific or subspecific level. On continental islands, they exhibit the same biogeographic patterns as other terrestrial vertebrates. The strong marine barriers within and around the Japanese islands have effectively restricted range expansion in these highly vagile animals. However, colonisation into oceanic islands with poor biotas seems to have led to the rapid generation of distinct but evolutionarily short-lived forms. To understand the biogeography of the Japanese birds in depth, more precise descriptions of phenotypic and genetic diversity and distribution ranges, particularly near the biogeographic borders, are necessary.

References

Abe H, Ishii N, Itoo T, Kaneko Y, Maeda K, Miura S, Yoneda M (2005) A guide to the mammals of Japan, 2nd edn. Tokai University Press, Hadano

BirdLife International (2015) Species factsheet: *Gorsachius goisagi*. Downloaded from http://www.birdlife.org on 09/11/2015

Choi C-Y, Nam H-Y (2008) Distribution of the Japanese Wagtail *Motacilla grandis* in Korea. Ornithol Sci 7(1):85–91

Cracraft J (1983) Species concepts and speciation analysis. In: Johnston R (ed) Current ornithology, vol 1. Springer, New York, pp 159–187. doi:10.1007/978-1-4615-6781-3_6

Dekker R, Dickinson E, Morioka H (2001) Systematic notes on Asian birds. 18. Some nomenclatural issues relating to Japanese taxa described in the Planches Coloriées (1820–1839) and Fauna Japonica, Aves (1844–1850). Zool Verh 335:199–214

del Hoyo J, Elliott A, Sargatal J, Cabot J (eds) (2010) Handbook of the birds of the world, vol 15. Lynx Edicions, Barcelona

Dong L, Wei M, Alström P, Huang X, Olsson U, Shigeta Y, Zhang Y, Zheng G (2015) Taxonomy of the Narcissus Flycatcher *Ficedula narcissina* complex: an integrative approach using morphological, bioacoustic and multilocus DNA data. Ibis 157(2):312–325. doi:10.1111/ibi.12238

Felsenstein J (1989) PHYLIP: phylogeny inference package (version 3.2). Cladistics 5(2): 164–166. doi:10.1111/j.1096-0031.1989.tb00562.x

Gooders J (1982) Collins British birds. William Collins, London

Hachisuka M (1925) A comparative hand list of the birds of Japan and the British isles. Cambridge University Press, Cambridge

Holt BG, Lessard J-P, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre P-H, Graham CH, Graves GR, Jønsson KA, Nogués-Bravo D, Wang Z, Whittaker RJ, Fjeldså J, Rahbek C (2013) An update of Wallace's zoogeographic regions of the world. Science 339(6115):74–78. doi:10.1126/science.1228282

Kerr KCR, Birks SM, Kalyakin MV, Red'kin YA, Koblik EA, Hebert PDN (2009) Filling the gap: COI barcode resolution in eastern Palearctic birds. Front Zool 6:29–29. doi:10.1186/1742-9994-6-29

Kuroda N (1932) A revision of the types of birds described by Japanese authors during the years 1923 to 1931. Novit Zool 37:384–405

McKay BD, Mays HL, C-T Y, Wan D, Higuchi H, Nishiumi I (2014) Incorporating color into integrative taxonomy: analysis of the varied tit (*Sittiparus varius*) complex in East Asia. Syst Biol. doi:10.1093/sysbio/syu016

Mearns B, Mearns R (1988) Biographies for bird watchers: the lives of those commemorated in Western Palearctic bird names. Academic Press, London

Merriam-Webster (1997) Merriam-Webster's geographical dictionary. Merriam-Webster, Springfield

Millien-Parra V, Jaeger J-J (1999) Island biogeography of the Japanese terrestrial mammal assemblages: an example of a relict fauna. J Biogeogr 26(5):959–972. doi:10.1046/j.1365-2699.1999.00346.x

Morioka H (1971) Alpine Avifauna of Hokkaido, Japan. Mem Natl Sci Mus 4:43–54

Morioka H (1974) Avifauna of the Ryukyu Islands and its origin. Mem Natl Sci Mus 7:203–211

Morioka H (1979) Taxonomic and distributional notes on Japanese birds: 1. Notes on *Turdus chrysolaus orii*. Tori 28(4):125–129. doi:10.3838/jjo1915.28.125

Morioka H (1990) Breeding birds of the Tokara Islands and their origin. Mem Natl Sci Mus 23: 151–166

Morioka H (1994) Subspecific status of certain birds breeding in Hokkaido. Mem Natl Sci Mus 27: 165–173

Morioka H, Sakane T (1980) Subalpine avifauna of the Ohmine mountain range in the Kii Peninsula, Japan. Mem Natl Sci Mus 13:53–58

Morioka H, Dickinson EC, Hiraoka T, Allen D, Yamasaki T (2005) Types of Japanese birds. Natl Sci Mus Monogr 28:1–154

Nakamura T, Nakamua M (1995) Bird's life in Japan with color pictures: birds of mountain, woodland and field. Hoikusha, Osaka

Nishiumi I, Morioka H (2009) A new subspecies of *Zoothera dauma* (Aves, Turdidae) from Iriomotejima, southern Ryukyus, with comments on *Z. d. toratugumi*. Bull Natl Mus Nat Sci Ser A Zool 35(2):113–124

Ota H (1998) Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Res Popul Ecol 40(2):189–204. doi:10.1007/BF02763404

Ota H (2000) The current geographic faunal pattern of reptiles and amphibians of the Ryukyu Archipelago and adjacent regions. Tropics 10(1):51–62. doi:10.3759/tropics.10.51

Parkin D, Knox A (2010) The status of birds in Britain and Ireland. Black, London

Saitoh T, Alström P, Nishiumi I, Shigeta Y, Williams D, Olsson U, Ueda K (2010) Old divergences in a boreal bird supports long-term survival through the Ice Ages. BMC Evol Biol 10:35. doi:10.1186/1471-2148-10-35

Saitoh T, Sugita N, Someya S, Iwami Y, Kobayashi S, Kamigaichi H, Higuchi A, Asai S, Yamamoto Y, Nishiumi I (2015) DNA barcoding reveals 24 distinct lineages as cryptic bird species candidates in and around the Japanese Archipelago. Mol Ecol Resour 15(1):177–186. doi:10.1111/1755-0998.12282

Seki S, Tokorozaki S, Mizoguchi F, Takagi S, Nakamura N, Crystal F (2011) Avifauna of the Tokara Islands, northern Ryukyu Archipelago. Bull For For Prod Res Inst 10(4):183–229

Sengoku S, Hikida T, Matsui M, Nakaya K (eds) (1996) The encyclopedia of the animals in Japan, vol. 5. Amphibians, reptiles, Chondrichthyes. Heibonsha, Tokyo

Short LL (1973) Notes on Okinawan birds and Ryukyu Island zoogeography. Ibis 115(2):264–267. doi:10.1111/j.1474-919X.1973.tb02642.x

Statistics Bureau Ministry of Internal Affairs and Communications (2015) Japan statistical yearbook 2015. http://www.stat.go.jp/data/nenkan/index1.htm. Accessed 10 June 2015

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. Mol Biol Evol 30(12):2725–2729. doi:10.1093/molbev/mst197

The American Ornithologists' Union (1919) Notes and news. Auk 36(4):628–636. doi:10.2307/4073424

The Ornithological Society of Japan (1974) Check-list of Japanese birds, 5th edn. Gakken, Tokyo

The Ornithological Society of Japan (2000) Check-list of Japanese birds, 6th edn. The Ornithological Society of Japan, Obihiro

The Ornithological Society of Japan (2012) Check-list of Japanese birds, 7th edn. The Ornithological Society of Japan, Sanda

The World Bank (2015) World development indicators. World Bank, Washington, DC. Accessed 8 July 2015

Vaurie C (1959) The birds of the Palearctic Fauna: order Passeriformes. Witherby, London

Vaurie C (1965) The birds of the Palearctic Fauna: non-Passeriformes. Witherby, London

Yamasaki T (2006) Taxonomic status of populations of the light-vented bulbul *Pycnonotus sinensis* (Gmelin, 1789) (Passeriformes: Pycnonotidae) in Taiwan and the southern Ryukyus. Zool Stud 45(2):168–179

Chapter 5
Historical Biogeography of the Terrestrial Reptiles of Japan: A Comparative Analysis of Geographic Ranges and Molecular Phylogenies

Taku Okamoto

Abstract The geographic ranges and divergence times of Japanese terrestrial reptiles and their close relatives were compared on the basis of recent taxonomic and molecular systematic studies. The comparison of geographic ranges suggested that the Japanese reptile fauna consists of three major biogeographic elements, those of the Southern Ryukyus, the Central Ryukyus, and the Japan Mainland, encompassing taxa endemic to each of these areas. In addition, some interchanges with southern China–Taiwan, Korea–northeastern China–far eastern Russia, and the Pacific islands may also have contributed to the Japanese reptile fauna. The comparison of geographic ranges of related taxa and their divergence times suggested that most of the Southern Ryukyu element was formed by isolation from the fauna of Taiwan and southern China during the Pliocene; the Central Ryukyu element was mostly formed by isolation from the faunas of Taiwan, China, and the Japan Mainland during the late Miocene, in addition to some quite old relict taxa dating back to the Eocene; and the Japan Mainland element was initially formed by isolation from the continental fauna during the middle Miocene, followed by secondary interchange in the Pliocene and Pleistocene.

Keywords Reptiles • Biogeography • Japan • Ryukyus • Divergence time • Molecular phylogeny

5.1 Introduction

More than 70 species and subspecies of terrestrial reptiles naturally occur in Japan, most of which are endemic to the country (Hikida 2002; Hikida and Ota 1997; Ota 1998; Sengoku et al. 1996). Japan constitutes the major part of the East Asian island

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area and encompasses several island groups with specific faunas. Therefore, biogeographic considerations are important for understanding the diversity of Japanese terrestrial reptiles.

The biogeography of Japanese terrestrial reptiles has been comprehensively discussed by several authors (Hikida 2002, 2003; Hikida et al. 1989, 1992; Hikida and Ota 1997; Ota 1998, 2000). Traditionally, the reptiles of the Japan Mainland have been regarded as part of the Palearctic element, and those of the Ryukyus as part of the Oriental element (Hikida et al. 1992). Hikida and Ota (1997) and Ota (1998, 2000), however, compared the taxonomic compositions of reptiles and amphibians between the island groups of Japan, Taiwan, and southern continental China, and clarified that the Okinawa and Amami Groups exhibited strong endemicity, whereas the Miyako and Yaeyama Groups had a certain affinity with Taiwan and the continent. Then, by modifying the paleogeographic hypothesis of Kizaki and Oshiro (1977), they proposed that the land areas of the Central and Southern Ryukyus were isolated from Taiwan and the continent in the Pliocene and Pleistocene, respectively.

These milestone works, however, focused almost exclusively on the Ryukyus, and the Japan Mainland reptiles have attracted little attention from those workers and other biogeographers. In addition, taxonomic and molecular systematic studies including Japanese reptiles have significantly progressed since 2000 (see the next section). Needless to say, the phylogenetic relationships and divergence times based on those molecular systematic studies are expected to improve the biogeographic considerations. In this chapter, the biogeographic patterns of Japanese terrestrial reptiles are compared on the basis of recent molecular and biogeographic work. From this, the historical biogeography of Japanese terrestrial reptiles is discussed.

5.2 Reviews of Each Taxon

Herein, each taxon of Japanese terrestrial reptiles is briefly reviewed focusing on its geographic range, ranges of closely related taxa, and divergence times between that taxon and its close relatives. Taxa with no molecular, taxonomic, or biogeographic studies after the review of Ota (1998) are not mentioned in this section (but appear in the tables). Geographic range information was obtained mainly from the following general references, in addition to the references for each taxon: Sengoku et al. (1996) for general descriptions of most of the Japanese taxa; Maenosono and Toda (2007) for ranges of taxa in the Ryukyus; Turtle Taxonomy Working Group (2014) for turtles; Xiang et al. (2009) for taxa occurring in Taiwan; and Zhao and Adler (1993) for taxa in China. Records representing nonnative and cryptogenic occurrences according to Ota et al. (2004), Toda and Yoshida (2005), and Kraus (2009) were excluded. In addition, some fossil reptiles of Neogene or later are briefly mentioned, when biogeographically significant (e.g., extinct species close to taxa of interest, or extant taxa found outside the current geographic range). The biogeographic pattern of each taxon is described using the geographic definitions presented in Fig. 5.1.

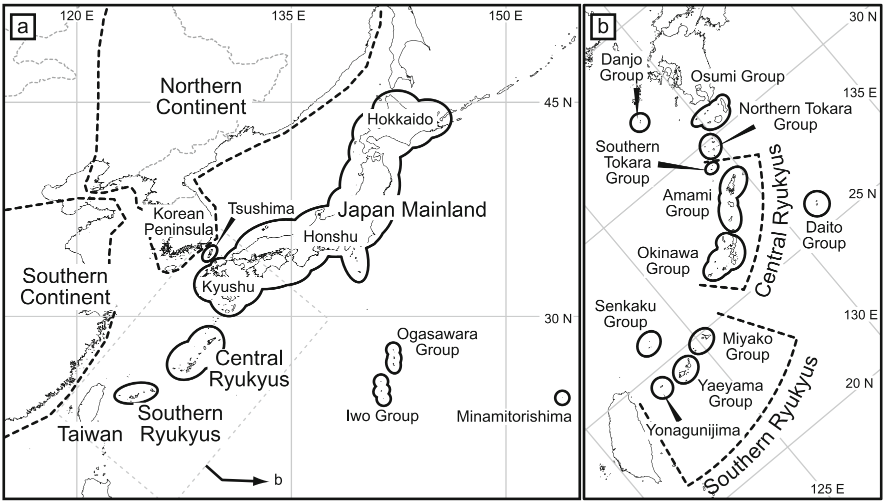

Fig. 5.1 (**a**) Geographic settings of Japan and adjacent regions used in this chapter. (**b**) Detailed geographic settings of the Ryukyus and other island groups used in this chapter

Initially, all the terrestrial reptiles naturally occurring in Japan were enumerated in tables based on the current taxonomic treatments. The endemic taxa for the Southern Ryukyus, the Central Ryukyus, and the Japan Mainland (see Fig. 5.1a for definitions of these areas) are listed in Tables 5.1, 5.2, and 5.3, respectively. Taxa endemic to other part of Japan and nonendemics are listed in Table 5.4. A total of 80 species and subspecies are recognized, and 66 of them (82.5 %) are endemic to some parts of Japan.

For phylogenetic positions and divergence times, the results of published molecular systematic studies were obtained. Divergence times estimated in the published works were accepted here regardless of dating methods. When a molecular study did not estimate divergence times but provided genetic distances or branch lengths based on cytochrome *b*, 12S, or 16S rRNA of mitochondrial DNA, divergence dates were roughly estimated by assuming simple molecular clocks. For lizards and snakes, the widely used divergence rates of 2 % to 4 % per million years (MY) for cytochrome *b* (Malhotra and Thorpe 2000; Poulakakis et al. 2005) and 0.6 % to 1.6 %/MY for 12S and 16S rRNA (0.3–0.4 times the rate of cytochrome *b*; Honda et al. 2014) were tentatively employed. For turtles, divergence times were estimated by cytochrome *b* divergences (branch lengths of Fig. 5.2 of Spinks et al. 2004 for Geoemydidae; distance matrix of Suzuki and Hikida 2014 for *Pelodiscus*) and divergence rate of 0.3% to 0.5 %/MY (Avise et al. 1992; Lenk et al. 1999).

Table 5.1 Geographic distributions, ranges of closely related taxa, and divergence times of taxa endemic to the Southern Ryukyus

	Range			Range of closely related taxa				
Taxa (families)	Yonaguni Is.	Yaeyama G.	Miyako G.	Within S Ryukyus	C Ryukyus	Taiwan	S China	Divergence times (MYA)
Wide-ranging								
Plestiodon kishinouyei (Scincidae)	+	+	+			+	+	1.5–5
Scincella boettgeri (Scincidae)	+	+	+			+		4.1–8.0
Dinodon rufozonatum walli (Colubridae)	+	+	+		+	+	+	Unknown
Elaphe taeniura schmackeri (Colubridae)		+	+			+?[b]	+?[b]	Unknown
Lycodon ruhstrati multifasciatus (Colubridae)		+	+			+?[b]	+?[b]	Unknown
Mauremys mutica kami (Geoemydidae)	+	+				+	+	4.4–7.3
Cuora flavomarginata evelynae (Geoemydidae)	+[a]	+				+	+	1.8–3.0
Japalura polygonata ishigakiensis (Agamidae)		+	+	+?[b]	+?[b]	+?[b]		Unknown
Yonaguni endemics								
Calamaria pavimentata miyarai (Colubridae)	+					+?[b]	+?[b]	Unknown
Elaphe carinata yonaguniensis (Colubridae)	+					+?[b]	+?[b]	Unknown
Japalura polygonata donan (Agamidae)	+			+?[b]	+?[b]	+?[b]		Unknown
Yaeyama endemics								

Plestiodon stimpsonii (Scincidae)		+			+	+	+	1.4–1.8 (*P. kuchinoshimensis*), 3–7.3 (*P. marginatus–oshimensis–stimpsonii–kuchinoshimensis–elegans* complex)
Takydromus dorsalis (Lacertidae)		+					+	2.9–9.0
Protobothrops elegans (Viperidae)		+				+	+	ca. 3
Pareas iwasakii (Pareatidae)		+				+?[e]		Unknown
Achalinus formosanus chigirai (Xenodermatidae)		+				+?[b]		Unknown
Sinomicrurus macclellandi iwasakii (Elapidae)		+				+?[b]	+?[b]	Unknown
Hebius ishigakiensis (Colubridae)		+		+?[c]	+?[c]			Unknown
Cyclophiops herminae (Colubridae)		+			+?[d]			
Miyako endemics								
Takydromus toyamai (Lacertidae)			+			+	+	2.7–7.3
Calamaria pfefferi (Colubridae)			+	+?		+?	+?	Unknown
Hebius concelarus (Colubridae)			+	+?[c]	+?[c]			Unknown

+, presence; +?, presence suggested by nonmolecular evidence

[a] Late Pleistocene occurrence of conspecific population was suggested by the fossil record, despite unknown subspecific position

[b] Geographic ranges of conspecific subspecies

[c] Based on assumption of monophyly of *Hebius ishigakiensis*, *H. concelarus*, and *H. pryeri* according to Ota and Iwanaga (1997) and Ota (1998)

[d] Based on assumption of monophyly of *Cyclophiops herminae and C. semicarinatus* suggested by Ota (1998)

[e] Based on assumption of monophyly of *Pareus iwasakii* and *P. formosensis* according to Ota et al. (1997) and Ota (1998)

Table 5.2 Geographic distributions, ranges of closely related taxa, and divergence times of taxa endemic to the Central Ryukyus

	Range				Range of closely related taxa					
Taxa (families)	Okinawa G.	Amami G.	S Tokara G.	N Tokara G.	Within C Ryukyus	S Ryukyu	Taiwan	S China	Other	Divergence times (MYA)
Almost equally close to multiple taxa										
Japalura p. polygonata (Agamidae)	+	+				+?[c]	+?[c]			Unknown
Plestiodon barbouri (Scincidae)	+	+			+	+	+	+	+(Japan Mainland)	5.5–14 (members of *P. latiscutatus* species group)
Takydromus smaragdinus (Lacertidae)	+	+	+			+	+	+	+(Japan Mainland, Northern Continent)	5–18
Dinodon semicarinatum (Colubridae)	+	+				+	+	+	+(NE China, Korea, Tsuhima)	Unknown
Protobothrops flavoviridis + *tokarensis* complex (2 species, Viperidae)	+	+	+			+	+	+		6–17
Sister taxa limited to Taiwan										
Sinomicrurus japonicus (3 subspecies, Elapidae)	+	+					+?[f]			Unknown
Ovophis okinavensis (Viperidae)	+	+					+			5–14
Sister taxa limited to the continent										
Geoemyda japonica (Geoemydidae)	+	+[a]						+		33.9–56.4

Goniurosaurus kuroiwae (4 subspecies) + *splendens* lineage (Eublepharidae)	+	+						+		40–65
Ateuchosaurus pellopleurus (Scincidae)	+	+	+	+				+?[g]		Unknown
Miscellaneous or unknown phylogenetic position										
Plestiodon marginatus (Scincidae)	+	+[b]		+	+	+	+	+		3–7.3 (*P. marginatus–oshimensis–stimpsonii–kuchinoshimensis–elegans* complex)
Plestiodon oshimensis (Scincidae)		+	+	+	+	+	+	+		Ditto
Plestiodon kuchinoshimensis (Scincidae)				+		+				1.4–1.8 (*P. stimpsonii*)
Hebius pryeri (Colubridae)	+	+				+?[d]				Unknown
Cyclophiops semicarinatus (Colubridae)	+	+	+			+?[e]				Unknown
Gekko shibatai (Gekkonidae)			+		Unknown					
Gekko vertebralis (Gekkonidae)		+	+		Unknown					
Gekko sp. 2 (Gekkonidae)	+				Unknown					

(continued)

Table 5.2 (continued)

Taxa (families)	Range				Range of closely related taxa					Divergence times (MYA)
	Okinawa G.	Amami G.	S Tokara G.	N Tokara G.	Within C Ryukyus	S Ryukyu	Taiwan	S China	Other	
Achalinus werneri (Xenodermatidae)	+	+			Unknown					
Opisthotropis kikuzatoi (Colubridae)	+				Unknown					

+, presence; +?, presence suggested by nonmolecular evidence

[a] Based on the assumption of the sister relationship of *Geoemyda japonica* and *G*. *amamiensis* according to Takahashi et al. (2007)

[b] Limited to two southernmost islands, Yoronjima and Okinoerabujima, from which *P*. *oshimensis* is absent

[c] Geographic ranges of conspecific subspecies

[d] Based on the assumption of monophyly of *H*. *ishigakiensis*, *H*. *concelarus*, and *H*. *pryeri* according to Ota and Iwanaga (1997) and Ota (1998)

[e] Based on the assumption of monophyly of *C*. *herminae* and *C*. *semicarinatus* suggested by Ota (1998)

[f] Based on the assumption of monophyly of *S*. *japonicus*, *S*. *hatori*, and *S*. *sauteri* suggested by Ota et al. (1999)

[g] Geographic range of the only congener *A*. *chinensis*

Table 5.3 Geographic distributions, ranges of close taxa, and divergence times of taxa endemic to the Japan Mainland and two exceptional taxa

Taxa (families)	Range			Range of closely related taxa						Divergence times (MYA)
	Hokkaido	Honshu–Kyushu	Other areas	C. Ryukyus	S. Ryukyus	Taiwan	S. China	Korea–NE China	Other	
Known phylogenetic positions										
Euprepiophis conspicillatus (Colubridae)	+	+				+	+			14–23
Mauremys japonica (Geoemydidae)		+[b]			+[b]	+	+	+ (Korea only)		11.5–19.3
Elaphe climacophora (Colubridae)	+	+	Tsushima			+	+	+	+(Wide area of Eurasia)	9–20
Elaphe quadrivirgata (Colubridae)	+	+						+		8–20
Takydromus tachydromoides (Lacertidae)	+	+	N Tokara	+	+	+	+	+		5–18
Plestiodon latiscutatus-japonicus-finitimus lineage (3 species, Scincidae)[a]	+	+		+	+	+	+			5.5–14 (other members of *P. latiscutatus* species-group
Rhabdophis tigrinus (Colubridae)		+				+	+	+		4–15
Gloydius blomhoffii (Viperidae)	+	+						+		1–7.3

(continued)

Table 5.3 (continued)

Taxa (families)	Range			Range of closely related taxa						Divergence times (MYA)
	Hokkaido	Honshu–Kyushu	Other areas	C. Ryukyus	S. Ryukyus	Taiwan	S. China	Korea–NE China	Other	
Hebius v. vibakari + *danjoensis* (Colubridae)		+					+?[c]	+?[c]		<1.5[d]
Unknown phylogenetic positions										
Dinodon orientale (Colubridae)	+	+		Unknown						
Gekko tawaensis (Gekkonidae)		+ (limited part)		Unknown						
Gekko yakuensis (Gekkonidae)		+ (limited part)		Unknown						
Gekko sp. 1 (Gekkonidae)		+ (limited part)		Unknown						

+, presence; +?, presence suggested by nonmolecular evidence

[a] *P. finitimus* occurs in far eastern Russia as well as in eastern Japan

[b] Several fossil taxa possibly belonging to both the Japanese and continental lineages are also known

[c] Geographic ranges of conspecific subspecies

[d] Estimated time of divergence of *Hebius vibakari ruthveni* and *Hebius* sp. based on a molecular clock assumption and cytochrome *b* phylogeny of Guo et al. (2014). The divergence time of *H. vibakari* subspecies may be less than the value given here

Table 5.4 Geographic ranges of taxa endemic to peripheral parts of Japan or occurring outside of Japan

	Range in Japan							Range outside Japan				
Taxa (families)	S Ryukyus	C Ryukyus	Senkaku	Mainland	Tsushima	Pacific islands	Daito	Taiwan	S China	Korea-NE China	Pacific	Other
Associated with southern continent												
Gekko hokouensis (Gekkonidae)	+	+	+	+(southern small part)				+	+			
Hemidactylus bowringii (Gekkonidae)	+	+						+	+			
Plestiodon elegans (Scincidae)			+					+	+			
Elaphe c. carinata (Colubridae)			+					+	+			
Achalinus spinalis (Xenodermatidae)				+					+			
Associated with Tsushima and northern continent												
Gloydius tsushimaensis (Viperidae)					+							
Scincella vandenburghi (Scincidae)					+					+		
Takydromus amurensis (Lacertidae)					+					+		
Pelodiscus maackii (Trionichidae)				+						+		

(continued)

Table 5.4 (continued)

Taxa (families)	Range in Japan							Range outside Japan				
	S Ryukyus	C Ryukyus	Senkaku	Mainland	Tsushima	Pacific islands	Daito	Taiwan	S China	Korea-NE China	Pacific	Other
Zootoca vivipara (Lacertidae)				+(northern small part)						+(northern small part)		Sakhalin, Euro-Siberian region
Associated with southern and northern continent												
Dinodon r. rufozonatum (Colubridae)			+		+			+	+	+		
Associated with Pacific islands												
Cryptoblepharus nigropunctatus (Scincidae)						+(Ogasawara Group, Iwo Group, Minamitorishima)						
Perochirus ateles (Gekkonidae)						+(Minamitorishima, Minamiiwojima of Iwo Group)					+	
Lepidodactylus lugubris (Gekkonidae)							+				+	Southeast Asian Continent, Indian Ocean, South America
Emoia a. atrocostata (Scincidae)	+(Miyako Group)										+	Southeast Asian Continent, Taiwan

Plestiodon finitimus is not listed here, because it is nearly endemic to Japan
+, presence

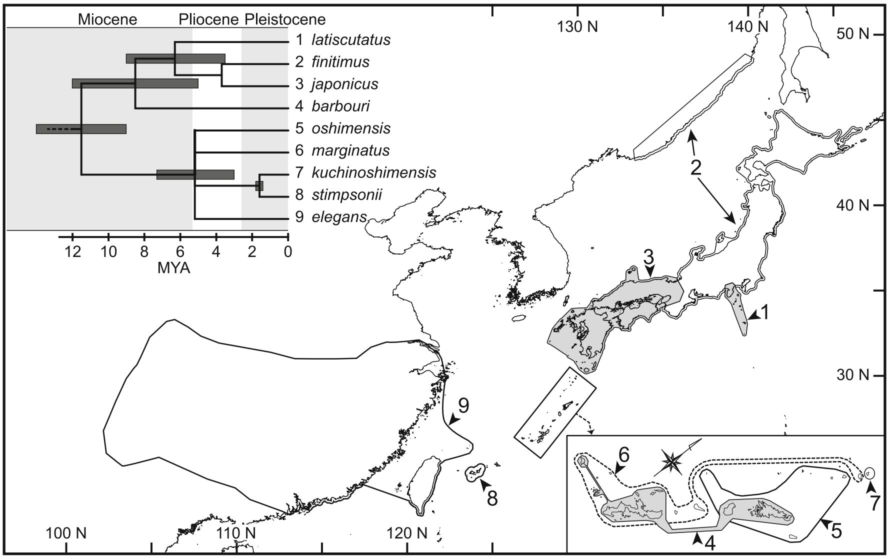

Fig. 5.2 Summarized time-calibrated phylogeny and geographic ranges of the lizards of the *Plestiodon latiscutatus* species group. The *error bars* in the phylogeny are credible intervals of divergence times obtained from Brandley et al. (2011) and Kurita and Hikida (2014a)

5.2.1 Turtles of the Family Geoemydidae

Mauremys japonica is a freshwater turtle endemic to the central and western parts of the Japan Mainland and Tsushima. The closest extant taxa are *M. sinensis* and the *M. reevesii–nigricans* lineage (Guillon et al. 2012; Spinks et al. 2004). The total geographic range of these taxa encompasses Korea, central to southern China ("China" in the remainder of this chapter means continental China), northern Vietnam, and Taiwan. The divergence time between *M. japonica* and other lineages was estimated to be 11.5 to 19.3 million years ago (MYA) according to the foregoing molecular clock. Although no fossil record is known for this species, several related fossil taxa have been found in Japan: two extinct species close to *M. japonica* from the Pleistocene, *M. yabei* from the Japan Mainland and *M. oshiroi* from the Miyako Group. In addition, fossils of several other related taxa are known from the Japan Mainland and the Osumi Group, consisting of a fossil similar to *M. nigricans* from Pliocene strata, and *M. sinensis* and its extinct relatives (*Ocadia* spp.) of Miocene to Pleistocene age (Hirayama 2001, 2006; Hirayama et al. 2007; Takahashi et al. 2013, 2015).

Mauremys mutica kami is a freshwater turtle endemic to the Yaeyama Group ("Yaeyama Group" in the remainder of this chapter does not include Yonagunijima, as described in Fig. 5.1b) and Yonagunijima. The sister group is the other subspecies *M. m. mutica*, which occurs in Taiwan, southern China, and northern Vietnam

(Spinks et al. 2004), with divergence at 4.4 to 7.3 MYA according to the molecular clock used herein.

Geoemyda japonica is a terrestrial turtle endemic to the Okinawa Group. The closest extant species is *G. spengleri* of southern China to northern Vietnam (Guillon et al. 2012; Spinks et al. 2004), with a divergence time of 33.9 to 56.4 MYA according to the molecular clock used herein. A fossil species, *G. amamiensis*, is known from the Pleistocene of Tokunoshima Island of the Amami Group, and is considered to be the sister taxon of *G. japonica* (Takahashi et al. 2007).

Cuora flavomarginata evelynae is a terrestrial box turtle endemic to the Yaeyama Group. Its sister taxon is the other subspecies, *C. f. flavomarginata*, of Taiwan and eastern China (the continental population is sometimes treated as another subspecies, *C. f. sinensis*) (Honda et al. 2002; Spinks et al. 2004), with a divergence time of 1.8 to 3.0 MYA according to the molecular clock used herein. Fossils of this species were recovered from Late Pleistocene strata of Yonagunijima, although the subspecific position of that material was not determined (Takahashi et al. 2008).

5.2.2 Soft-Shell Turtles of the Family Trionychidae

According to Suzuki and Hikida (2014), the freshwater soft-shell turtle *Pelodiscus maackii* (sensu Fritz et al. 2010; Turtle Taxonomy Working Group 2014) may naturally occur in the Japan Mainland, although the entire Japanese population is sometimes regarded as nonnative (Turtle Taxonomy Working Group 2014). The suggestion of Suzuki and Hikida (2014) is adopted here. This species occurs in the central to western Japan Mainland, Korea, northeastern China, and far eastern Russia. The populations of the Ryukyus are nonnative (Sato and Ota 1999). This species is almost equally close to two continental congeners, *P. sinensis* and *P. parviformis*, which are found in central to southern China, Taiwan, and northern Vietnam, with a divergence time of 5.0 to 8.3 MYA according to the molecular clock used herein.

5.2.3 Geckos of the Family Gekkonidae

Seven species of common geckos of the genus *Gekko* naturally occur in Japan: *Gekko hokouensis* in the southern part of the Japan Mainland, the entire Ryukyus, Taiwan, and southern China; three species in limited parts of the western Japan Mainland, *G. tawaensis*, *G. yakuensis*, and an undescribed species in western Kyushu and adjacent islands (*Gekko* sp. 1 herein, e.g., Matsuo 2005); *G. shibatai* in southern Tokara and *G. vertebralis* mainly in the Amami Group (Toda et al. 2008); and another undescribed species in the Okinawa Group (*Gekko* sp. 2 herein Toda et al. 2001; Toda 2008). *Gekko japonicus* is widespread in the Japan Mainland but is likely to be nonnative (Toda and Yoshida 2005). With the exception of *G. hokouensis*, all these species have mutually exclusive geographic ranges. Although these species may belong to the *G. japonicus* species group (sensu Rösler et al. 2011) that is found in Taiwan, central and southern China, and part of Indochina, the phylogenetic positions of most of the species have not yet been studied.

Lepidodactylus lugubris is an all-female parthenogenetic gecko with a wide geographic range including many tropical and subtropical islands of the Indian and Pacific Oceans, Southeast Asia, and Central to South America showing geographic variation (Ineich 1999), although some populations are nonnative (Kraus 2009). The Daito Group population encompasses multiple specific clonal strains and is regarded as the only natural population in Japan (Yamashiro et al. 2000).

5.2.4 Geckos of the Family Eublepharidae

Goniurosaurus kuroiwae and *G. splendens* are eyelid ground geckos endemic to the Central Ryukyus. The former species consists of four extant and one extinct subspecies with allopatric geographic ranges mainly in the Okinawa Group (Honda et al. 2014; Nakamura et al. 2014). The current subspecific classification is not consistent with the molecular phylogeny. *Goniurosaurus splendens* is endemic to Tokunoshima Island of the Amami Group. The sister relationship of these two species is strongly supported, with deep divergence (10–20 MYA; Honda et al. 2014). Several other congeners are known from southern China and northern Vietnam. Molecular studies suggested that the Ryukyus lineage is quite deeply divergent from the continental species (40–65 MYA; Honda et al. 2014; Wang et al. 2014).

5.2.5 Lizards of the Family Agamidae

Japalura polygonata is an arboreal lizard with four subspecies: *J. p. polygonata* from the Okinawa and Amami Groups; *J. p. ishigakiensis* from the Miyako and Yaeyama Groups; *J. p. donan* from Yonagunijima (Ota 2003); and *J. p. xanthostoma*, which is endemic to northern Taiwan. The phylogenetic relationships of these subspecies and the close taxa of this species have not yet been clarified by molecular studies.

5.2.6 Lizards of the Family Scincidae

The *Plestiodon latiscutatus* species group (sensu Brandley et al. 2012; Hikida 1993) is a monophyletic group of blue-tailed lizards with three lineages containing a total of nine species. The Japan Mainland lineage has a crown divergence of 3.5 to 9 MYA, and includes *P. latiscutatus*, *P. japonicus*, and *P. finitimus* of the Japan Mainland, several adjacent islands, and Far Eastern Russia with parapatric geographic ranges (Motokawa and Hikida 2003; Okamoto et al. 2006; Okamoto and Hikida 2012). The second lineage is *P. barbouri*, which occurs in the Okinawa and Amami Groups. The third lineage is the Ryukyu–Taiwan–China lineage with a crown divergence time of 3 to 7.3 MYA, encompassing *P. kuchinoshimensis*, which is limited to part of the northern Tokara Group and diverged from *P. stimpsonii* at 1.4 to 1.8 MYA; *P. oshimensis*, which occurs in most parts of the Amami Group to part of northern Tokara; *P. marginatus* of the Okinawa Group, the southern small part of the Amami Group, and part of northern Tokara Group; *P. stimpsonii*, which is endemic to the Yaeyama Group; and *P. elegans* in the Senkaku Group and Taiwan. The Japan Mainland lineage and *P. barbouri* are probably monophyletic with a divergence time of 5 to 12 MYA. The divergence between these lineages and the Ryukyu–Taiwan–China lineage dates back to 9 to 14 MYA (Brandley et al. 2011, 2012; Kurita and Hikida 2014a, b). The phylogeny, divergence times, and geographic ranges of these species are summarized in Fig. 5.2.

Plestiodon kishinouyei is a large-bodied blue-tailed lizard endemic to the Southern Ryukyus. The closest relative of this species is *P. chinensis*, which is known from Taiwan, central to southern China, and a small part of the Korean Peninsula, with a divergence time of 1.5 to 5 MYA (Brandley et al. 2011).

Scincella vandenburghi is a small ground lizard that is found in Tsushima Island, the southern half of the Korean Peninsula, and Cheju Island (Chen et al. 2001a). The phylogenetic position of this species is unknown.

Scincella boettgeri is a small ground lizard endemic to the Southern Ryukyus. The sister species is *S. formosensis*, which is endemic to Taiwan, with divergence at 4.1 to 8.0 MYA (Koizumi et al. 2014). The genetic divergence between the populations of the Miyako–Yaeyama Groups and Yonagunijima is as large as that between this species and *S. formosensis* (Koizumi et al. 2014), despite the lack of significant intraspecific morphological differences (Chen et al. 2001b).

Cryptoblepharus nigropunctatus is a snake-eyed lizard endemic to the Ogasawara Group, the Iwo Group, and Minamitorishima Island (Toda 2014). Although the comprehensive phylogeny of this genus has not been clarified, its distinct intraspecific variation and moderate divergence from *C. novocaledonicus* of New Caledonia were clarified by Hayashi et al. (2009).

5.2.7 Lizards of the Family Lacertidae

Zootoca vivipara is a ground lizard that occurs widely in the northern part of Hokkaido, Sakhalin, far eastern Russia, and northeastern Asia to Europe. This species encompasses multiple oviparous and viviparous lineages that diversified during the Pleistocene (Surget-Groba et al. 2001). The Japanese population belongs to the "eastern viviparous" group of Sakhalin and eastern Russia to eastern Europe (Takeuchi et al. 2013).

Five species of grass lizards of the genus *Takydromus* occur in Japan: *T. tachydromoides*, which is endemic to the Japan Mainland and the northern Tokara Group; *T. smaragdinus* of the Central Ryukyus; *T. toyamai* of the Miyako Group; *T. dorsalis* of the Yaeyama Group; and *T. amurensis*, which has a range of Tsushima, the Korean Peninsula, northeastern China, and far eastern Russia. The phylogeny, divergence times, and geographic ranges of these species and close relatives are summarized in Fig. 5.3, using information from several molecular studies (Lin et al. 2002; Lue and Lin 2008; Ota et al. 2002; Tang and Chen 2006; Tseng et al. 2015). Because the divergence time estimation by Tseng et al. (2015) was limited to a few species, all the divergence times were estimated based on the molecular clock used herein and genetic distances obtained from Lin et al. (2002) for consistency. The phylogenetic positions of *T. tachydromoides* and *T. smaragdinus* are ambiguous, with deep divergences from other species (5 to

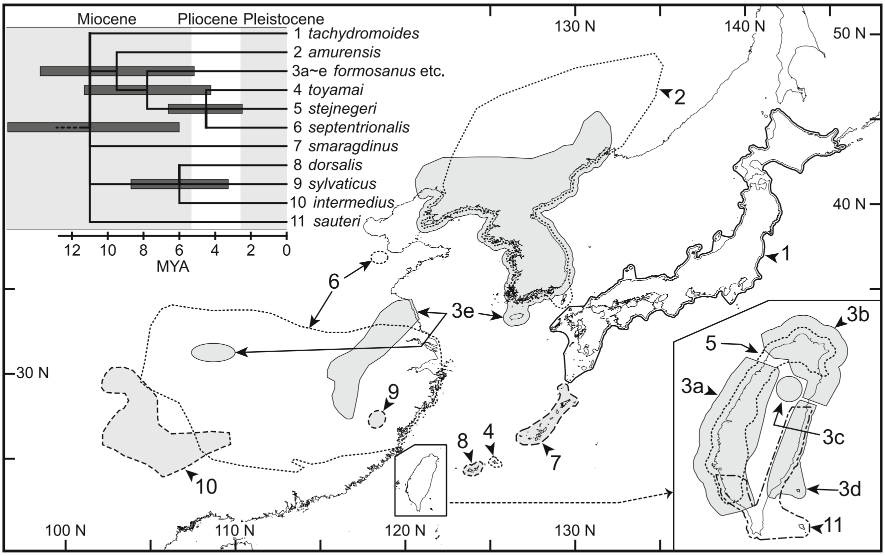

Fig. 5.3 Summarized time-calibrated phylogeny and geographic ranges of the Japanese species and their close relatives of the lizard genus *Takydromus*: (**a**) *T. formosanus*; (**b**) *T. viridipunctatus*; (**c**) *T. hsuehshanensis*; (**d**) *T. luyeanus*; (**e**) *T. wolteri*. The *error bars* in the phylogeny represent the lower and upper limits of divergence times based on genetic distances from Lin et al. (2002) and the molecular clock assumed here

18 MYA). *Takydromus toyamai* is close to *T. stejnegeri* from Taiwan and *T. septentrionalis* from central to southern China, with divergence at 2.4 to 7.3 MYA. *Takydromus dorsalis* is close to *T. sylvaticus* and *T. intermedius*, both of which are known in southern China, with divergence at 2.9 to 9 MYA. *Takydromus amurensis* is the sister taxon of the assemblage encompassing the *T. toyamai–stejnegeri–septentrionalis* lineage (see above) and the lineage of four Taiwanese species (*T. hsueshanensis*, *T. viridipunctatus*, *T. formosanus*, and *T. luyeanus*) and *T. wolteri*, which is known from the Korean Peninsula, central and northeastern China, and far eastern Russia, with deep divergence (4.9 to 16 MYA). *Takydromus sauteri* of Taiwan may also belong to the monophyletic group that includes these species, with divergence at 5 to 18 MYA from other species.

5.2.8 Snakes of the Family Colubridae

Elaphe quadrivirgata and *E. climacophora* are common ratsnakes that are widespread in the Japan Mainland and on several islets. In addition, the latter species occurs in Tsushima. Several molecular systematic studies failed to reconstruct well-supported relationships within *Elaphe* (Burbrink and Lawson 2007; Chen et al. 2014a; appendix S2 of Kuriyama et al. 2011; Utiger et al. 2002). Several studies have inferred a sister relationship between *E. quadrivirgata* and *E. schrenckii*, which is found in Korea, northeastern China, and far eastern Russia, with divergence at 8 to 20 MYA. The divergence of *E. climacophora* from other species may date back to 9 to 20 MYA, despite its unknown phylogenetic position.

Elaphe carinata is a ratsnake encompassing two subspecies: *E. c. yonaguniensis*, which is endemic to Yonagunijima, and *E. c. carinata* of the Senkaku Group, Taiwan, southern China, and northern Vietnam. The phylogeny and divergence dates of these subspecies have not yet been studied based on molecular data. Although a well-supported *Elaphe* phylogeny is not yet available (see above), this species is also deeply divergent from other congeners (13–20 MYA) (Burbrink and Lawson 2007; Chen et al. 2014a; appendix S2 of Kuriyama et al. 2011).

Elaphe taeniura schmackeri (recently often placed in *Orthriophis*) is a ratsnake endemic to the Southern Ryukyus. Eight other subspecies occur in Taiwan, a wide area of central to southern China, northeastern India, Bhutan, Indochina, the Malay Peninsula, Borneo, and Sumatra. The phylogenetic relationships between these subspecies are unknown. This species is deeply divergent (7–16 MYA) from the other three species placed in *Orthriophis*, which are known from southern China, India, Nepal, Myanmar, and Vietnam (Burbrink and Lawson 2007; Kuriyama et al. 2011; Utiger et al. 2002).

Euprepiophis conspicillatus is a ratsnake endemic to the Japan Mainland, and is the sister taxon of the *E. mandarinus–perlaceus* lineage that occurs in Taiwan, southern China, northeastern India, and northern Indochina, with deep divergence at 14 to 22 MYA (Burbrink and Lawson 2007; Chen et al. 2014a, b; Kuriyama et al. 2011).

Dinodon semicarinatum is an odd-tooth banded snake endemic to the Okinawa and Amami Groups. Another congener, *Dinodon rufozonatum*, consists of two subspecies: *D. r. rufozonatum* of Tsushima, the Senkaku Group, Taiwan, Korea, central to southern China, and northeastern Indochina; and *D. r. walli*, which is endemic to the Southern Ryukyus. These species are close to *D. flavozonatum* and *Lycodon futsingensis*, which are found in southeastern China to northern Indochina, although the relationships between these species and their degrees of divergence have not been ascertained (Guo et al. 2013).

Lycodon ruhstrati multifasciatus is a banded wolf snake endemic to the Miyako and Yaeyama Groups. Two other subspecies are present in Taiwan, central to southern China, and northern Vietnam (Vogel et al. 2009). Although the relationships of these subspecies have not yet been assessed with molecular data, this species (represented by continental samples) is close to *L. butleri*, *L. liuchengchaoi*, *L. multizonatus*, *L. synaptor*, and *L. fasciatus*, which occur in southern China, northeastern India, Indochina, and the Malay Peninsula with unknown degrees of divergence (Guo et al. 2013; Lei et al. 2014).

Rhabdophis tigrinus is a rear-fanged venomous snake that is endemic to the Japan Mainland except for Hokkaido. The closest and second closest species are *R. lateralis* (4–11 MYA divergence) that is found in the Korean Peninsula, a wide area of China, and far eastern Russia, and *R. formosanus* (6–15 MYA divergence) of Taiwan, respectively (Takeuchi et al. 2012, 2014).

Hebius (formerly *Amphiesma*) *vibakari* is a keelback snake with three subspecies: *H. v. vibakari*, known from the Japan Mainland with the exception of Hokkaido; *H. v. danjoensis* that is endemic to Oshima Island of the Danjo Group; and *H. v. ruthveni*, which occurs in the Korean Peninsula, northeastern China, and far eastern Russia. The phylogenetic relationships between the subspecies have not yet been studied using molecular data. On the basis of a molecular phylogeny (Guo et al. 2014) and the foregoing molecular clock assumption, this species (represented by continental subspecies) is close to a population with unknown taxonomic status ("*Amphiesma* sp." of Guo et al. 2014) that is found in Jiangxi, southeastern China, and seemingly diverged at 0.8 to 1.5 MYA. Assuming monophyly of *H. vibakari*, the divergence among its subspecies should be younger than 1.5 MYA. This lineage is the sister of *H. maximus* (sensu Guo et al. 2014) from southern China with divergence at 3 to 6.5 MYA.

5.2.9 Snakes of the Family Viperidae

Gloydius blomhoffii and *G. tsushimaensis* are small pitvipers that are endemic to the Japan Mainland and Tsushima, respectively. According to several molecular systematic studies (Fig. S2 of Fenwick et al. 2011; Paik et al. 1993; Xu et al. 2012), these species are monophyletic with *G. ussuriensis* and *G. brevicaudus*, which occur in Korea, central and northeastern China, and Far Eastern Russia. However, these studies did not agree on the relationships between these species. Given the ambiguity of some voucher information of Fenwick et al. (2011) and the consistency of phylogenies between Paik et al. (1993) and Xu et al. (2012), the results of the latter two studies appear to be more credible. According to those results, *G. blomhoffii* is the sister taxon of *G. ussuriensis* with divergence at 1.05–7.33 MYA. *Gloydius tsushimaensis* is the sister taxon of this lineage; however, its divergence time is unknown because it was not included in the molecular dating of Xu et al. (2012). The crown divergence of the four species may date back to 3.41 to 12.67 MYA.

Protobothrops elegans is a pitviper endemic to the Yaeyama Group. This species is close to *P. mucrosquamatus*, which is found in Taiwan, southern China, northern Indochina, and northeastern India, and *P. maolanensis*, which is known from a limited part of southern China (Liu et al. 2012; Zhang et al. 2013). The divergence between *P. elegans* and *P. mucrosquamatus* was at about 3 MYA (Fenwick et al. 2011).

Protobothrops flavoviridis and *P. tokarensis* are pitvipers endemic to the Okinawa–Amami Groups and the southern Tokara Group, respectively. The latter is phylogenetically nested within the former: *P. flavoviridis* of the Amami Group is closer to *P. tokarensis* than to the Okinawa Group populations (Malhotra and Thorpe 2004; Toda et al. 1999). The divergence time between *P. flavoviridis* of the Amami Group and *P. tokarensis* was estimated to be about 1 MYA (Fenwick et al. 2011). The divergence of this lineage and the Okinawa populations may have been at about 4 MYA, judged from the dendrogram and genetic distances of Toda et al. (1999) and the divergence times of *P. elegans* versus *P. mucrosquamatus* and *P. tokarensis* versus the Amami populations of Fenwick et al. (2011), as already mentioned. The *P. flavoviridis–tokarensis* complex is monophyletic with the *P. elegans–mucrosquamatus–maolanensis* lineage (see above) and the *P. jerdonii–xiangchengensis–daishanensis–cornutus* lineage of northeastern India, northern Vietnam, and central to southern China. The crown divergence of this group was at 6 to 17 MYA, although the relationship between the three lineages remains unclear (Fenwick et al. 2011; Liu et al. 2012; Malhotra and Thorpe 2004; Tu et al. 2000; Wüster et al. 2008; Zhang et al. 2013).

Ovophis okinavensis is a pitviper endemic to the Okinawa and Amami Groups. The sister species is *Trimeresurus gracilis*, which is endemic to alpine areas of Taiwan, with a divergence time of 5–14 MYA (Fenwick et al. 2011; Malhotra and Thorpe 2004; Tu et al. 2000; Wüster et al. 2008).

5.3 Discussion: General Biogeographic Patterns

As mentioned in the previous section, most of the Japanese reptiles are endemic to Japan. Most of these endemics are confined to one of three areas: the Southern Ryukyus, the Central Ryukyus, and the Japan Mainland, with a few exceptions.

These three areas can be recognized as distinct areas of endemism, as discussed by Hikida and Ota (1997) and Ota (1998). Using the geographic diversification patterns and divergence times, the historical biogeography of these three areas is discussed next.

The diversification patterns of the Southern Ryukyu endemic taxa are listed in Table 5.1. As pointed out by previous authors, the closest relatives of most species are found in Taiwan and southern China. In this region, the local endemicity of Yonagunijima Island, the Yaeyama Group, and the Miyako Group can additionally be recognized. The difference between the Yaeyama and Miyako Groups has already been discussed in previous studies. The endemicity of Yonagunijima was suggested in recent works, such as Ota (2003) and Koizumi et al. (2014). Those endemic taxa do not exhibit exclusive monophyly within the Southern Ryukyus in most cases, which implies that the local endemicity was not formed by diversification within this region, but by differential diversification from vicariants in Taiwan and China.

The estimated divergence times of the Southern Ryukyus and Taiwan–China lineages were roughly Pliocene for most taxa, as pointed out by Koizumi et al. (2014). This congruence suggests vicariance between the Southern Ryukyus and Taiwan–China during the Pliocene, which is apparently older than the Pleistocene vicariance assumed by Hikida and Ota (1997) and Ota (1998).

The diversification patterns of the Central Ryukyu endemic taxa (and some relatives) are listed in Table 5.2. Several previous studies (Honda et al. 2014; Toda et al. 1999) suggested additional local endemicity of the Amami and Okinawa Groups formed by divergence within the Central Ryukyus. However, the divergence time estimates for the Amami versus Okinawa lineages are currently limited to a few groups and are seemingly not congruent (e.g., 10–20 MYA for *Goniurosaurus*; 4 MYA for *Protobothrops*). The currently available data appear to be inadequate for further interpretation, and additional studies are required to clarify this issue.

Several Central Ryukyu lineages seemed to have two or more close lineages in Taiwan, China, and some other regions with similar degrees of divergence (e.g., *Plestiodon barbouri*, 5.5–14 MYA; *Takydromus smaragdinus*, 5–18 MYA; and *Protobothrops flavoviridis–tokarensis*, 6–17 MYA). The divergence times of most of these groups appeared to be concordantly around late Miocene time (Table 5.2). Although *Ovophis okinavensis* has a sister species limited to Taiwan, late Miocene (5–14 MYA) divergence was again suggested. Thus, a major part of the Central Ryukyu endemic lineage was considered to have been formed by isolation from other land areas around the late Miocene. Again, this timing is older than the Pliocene vicariance assumed by Hikida and Ota (1997) and Ota (1998).

Some other Central Ryukyus lineages, however, exhibited exceptional patterns. *Geoemyda* and *Goniurosaurus*, which possess sister taxa limited to southern China to northern Vietnam, exhibited extremely deep divergences dating back to the Eocene. This pattern can be interpreted as old relicts. Molecular assessment of another group exhibiting a similar disjunct pattern, short-legged lizards of the genus *Ateuchosaurus*, is important for further consideration. In contrast, *Plestiodon* (except for *P. barbouri*) seemed to exhibit exceptionally shallow divergences. The divergence between *P. stimpsonii* and *P. kuchinoshimensis* (1.4–1.8 MYA, early Pleistocene) may have occurred by long overseas dispersal (Kurita and Hikida 2014a) and the exceptional date was not unexpected. The Pliocene divergence (3–7.3 MYA) of Central Ryukyu taxa (*P. marginatus* and *P. oshimensis*) and Southern Ryukyu–Taiwan taxa (*P. stimpsonii* and *P. elegans*) also appeared to be shallower than those of other taxa. Although Hikida and Motokawa (1999) inferred divergence of these taxa by Pleistocene overseas dispersal between the Southern and Central Ryukyus after Pliocene isolation of land areas, Kurita and Hikida (2014a) negated their hypothesis and proposed divergence by Pliocene vicariance on the basis of molecular dating. However, the present comparison seemed to support the scenario of Hikida and Motokawa (1999) with modification of the dates of the events, that is, late Miocene vicariance followed by Pliocene dispersal of the ancestors of *P. marginatus* and *P. oshimensis*. Another exceptional pattern, exclusive affinity of the Southern and Central Ryukyus, was exemplified by the possible monophyly of *Hebius* of the Ryukyus (Ota 1998; Ota and Iwanaga 1997) and the Pleistocene geographic range of the fossil turtle *Manouria oyamai* (Southern and Central Ryukyus; Takahashi et al. 2008). This issue requires further consideration based on molecular systematic and paleontological studies including both Taiwanese and continental materials.

The taxa almost endemic to the Japan Mainland are listed in Table 5.3. Most species were widely distributed in the mainland, despite the absence of some species from Hokkaido. Although three *Plestiodon* species occur in limited areas (Fig. 5.2), the whole range of this entire monophyletic group encompasses the entire mainland. Thus, the range of the entire lineage can be interpreted as showing a pattern similar to those of other taxa. In contrast, the geographic ranges of *Gekko* species seemed quite exceptional compared to other reptiles.

Divergences between the majority of the Japan Mainland endemic reptiles and close relatives found in Taiwan and wide areas of China in most cases seemed to date back to the middle Miocene (e.g., *Mauremys japonica*, 11.5–19.3 MYA; *Elaphe* spp., 8–20 MYA), whereas some others diverged in Pliocene to Pleistocene times (*Gloydius blomhoffii*, 1–7.3 MYA; and *Hebius vibakari*, <1.5 MYA) (Table 5.3). Thus, the Japan Mainland endemicity may have been initially formed by isolation in the middle Miocene and subsequently modified by secondary interchange with the continental fauna in the Pliocene and Pleistocene. Although more precise estimation of divergence times is needed, this scenario appears to be consistent with some fossil records of continental living species from the late Pliocene of the Japan Mainland (e.g., the Chinese alligator *Alligator sinensis* and the big-headed turtle *Platysternon megacephalum*; Aoki 2001; Hirayama 2001). Also, the sympatric occurrence of the fossil turtles *Mauremys yabei* (close to the extant Japanese species *M. japonica*) and *Ocadia nipponica* (close to the extant continental species *M. sinensis*) in Pleistocene strata (Hirayama et al. 2007) can be explained by secondary interchange after Miocene divergence.

The geographic ranges of the taxa limited to peripheral parts of Japan and nonendemics (Table 5.4), could be classified into three groups: northern continent, southern continent (ranges are roughly delineated in Fig. 5.1a), and Pacific islands. Thus, some faunal interchanges with these regions have contributed to Japanese reptile diversity, in addition to the major biogeographic elements already discussed. For further discussion of these taxa, the biogeographic structure of the continent (Chen 2009; Zhang and Zhao 1978) and Pacific islands should be taken into account.

5.4 Conclusions and Future Prospects

The analysis performed in this study suggested the following scenario: the major part of the Southern Ryukyu fauna was formed by isolation from the fauna of Taiwan and southern China during the Pliocene; the Central Ryukyu fauna was formed by isolation from fauna of the other land areas in the late Miocene, and also encompasses a few relicts dating back to the Eocene; and the Japan Mainland fauna was initially formed by divergence from the continental fauna in the middle Miocene, and secondary interchange with the continent may have occurred during the Pliocene and Pleistocene. Additional overseas dispersal (e.g., *Plestiodon* of the Central Ryukyus) and some interchanges with the northern and southern continent and the Pacific islands, have also contributed to the present diversity of Japanese reptiles.

The present analysis supported young isolation between the Southern Ryukyus from Taiwan–China and older isolation of the Central Ryukyus from other regions, as suggested by Hikida and Ota (1997) and Ota (1998). However, the ages of isolations estimated here are clearly older: Pliocene and late Miocene for the Southern and Central Ryukyus, respectively. In previous studies, estimation of the ages of the events depended on the paleogeographic hypothesis of Kizaki and Oshiro (1977) with modification, which was one of several competing paleogeographic hypotheses, as discussed in Ota (1998). In contrast, the basis for the present estimates is a consensus of multiple independent estimates of divergence times. Thus, the present hypothesis seems more convincing. In addition, the present analysis suggested the coexistence of older (Eocene) and younger (late Miocene) elements in the Central Ryukyus. This discovery also exemplifies the advantage of explicit comparison of divergence times.

However, the present conclusion depends on some nontrivial assumptions, such as a simple molecular clock, little error in genetic distances, and monophyly of terminal taxa of the current classification. In addition, consideration of paleogeography was completely omitted. Additional improvements to the present hypothesis that take these issues into account are required. In addition, some matters could not be discussed here; for example, the biogeographic relationship between the Ryukyus, Taiwan, and China was not addressed. Although some taxa appear to exemplify a close affinity between the Southern and/or the Central Ryukyus and Taiwan + China (e.g., *Mauremys mutica* and the *Protobothrops elegans* lineage), others imply exclusive affinities of the Ryukyus and Taiwan (e.g., *Ovophis* *okinavensis* and *Scincella boettgeri*). This matter deserves further consideration, and requires additional molecular assessments of the taxa implying a Ryukyus–Taiwan affinity (e.g., *Japalura polygonata* and *Sinomicrurus japonicus*). Thus, further accumulation of appropriate molecular studies, in addition to the taxonomy of living and fossil taxa and consideration of paleogeography, will improve the biogeographic understanding of Japanese reptile diversity.

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References

Aoki R (2001) The crocodilian fossils from the Tsubusagawa Formation (Pliocene) of Japan. Research Report of the Lake Biwa Museum Project Office 18:97–109 (in Japanese with English abstract)

Avise JC, Bowen BW, Lamb T, Meylan AB, Bermingham E (1992) Mitochondrial DNA evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in the Testudines. Mol Biol Evol 9(3):457–473

Brandley MC, Wang Y, Guo X, Nieto Montes de Oca A, Fería-Ortíz M, Hikida T, Ota H (2011) Accommodating heterogenous rates of evolution in molecular divergence dating methods: an example using intercontinental dispersal of *Plestiodon* (*Eumeces*) lizards. Syst Biol 60(1):3–15

Brandley MC, Ota H, Hikida T, Nieto Montes de Oca A, Fería-Ortíz M, Guo X, Wan Y (2012) The phylogenetic systematics of blue-tailed skinks (*Plestiodon*) and the family Scincidae. Zool J Linn Soc 165:163–189

Burbrink FT, Lawson R (2007) How and when did Old World ratsnakes disperse into the New World? Mol Phylogenet Evol 43:173–189

Chen Y (2009) Conservation biogeography of the snake family Colubridae of China. North-West J Zool 5(2):251–262

Chen S, Hikida T, Han S, Shim J, Oh H, Ota H (2001a) Taxonomic status of the Korean populations of the genus *Scincella* (Squamata: Scincidae). J Herpetol 35(1):122–129

Chen S, Ota H, Hikida T (2001b) Geographic variation in the two smooth skinks, *Scincella boettgeri* and *S. formosensis* (Squamata: Scincidae), in the subtropical East Asian islands. Zool Sci 18:115–130

Chen X, McKelvy AD, Grismer LL, Matsui M, Nishikawa K, Burbrink FT (2014a) The phylogenetic position and taxonomic status of the rainbow tree snake *Gonyophis margaritatus* (Peters, 1871) (Squamata: Colubridae). Zootaxa 3881(6):532–548

Chen X, Jiang K, Guo P, Huang S, Rao D, Ding L, Takeuchi H, Che J, Zhang Y, Myers EA, Burbrink FT (2014b) Assessing species boundaries and the phylogenetic position of the rare Szechwan ratsnake, *Euprepiophis perlaceus* (Serpentes: Colubridae), using coalescent-based methods. Mol Phylogenet Evol 70:130–136

Fenwick AM, Greene HW, Parkinson CL (2011) The serpent and the egg: unidirectional evolution of reproductive mode in vipers? J Zool Syst Evol Res 50(1):59–66

Fritz U, Gong S, Auer M, Kuchling G, Schneeweiß N, Hundsdörfer AK (2010) The world's economically most important chelonians represent a diverse species complex (Testudines: Trionychidae: *Pelodiscus*). Org Divers Evol 10(3):227–242

Guillon J, Guéry L, Hulin V, Girondot M (2012) A large phylogeny of turtles (Testudines) using molecular data. Contrib Zool 81(3):147–158

Guo P, Zhang L, Liu Q, Pyron RA, Jiang K, Burbrink FT (2013) *Lycodon* and *Dinodon*: one genus or two? Evidence from molecular phylogenetics and morphological comparisons. Mol Phylogenet Evol 68:144–149

Guo P, Zhu F, Liu Q, Zhang L, Li JX, Huang YY, Pyron RA (2014) A taxonomic revision of the Asian keelback snakes, genus *Amphiesma* (Serpentes: Colubridae: Natricinae), with description of a new species. Zootaxa 3873(4):425–440

Hayashi F, Shima A, Horikoshi K, Kawakami K, Segawa RD, Tadashi A, Suzuki T (2009) Limited overwater dispersal and genetic differentiation of the snake-eyed skink (*Cryptoblepharus nigropunctatus*) in the Oceanic Ogasawara Islands, Japan. Zool Sci 26:543–549

Hikida T (1993) Phylogenetic relationships of the skinks of the genus *Eumeces* (Scincidae: Reptilia) from East Asia. Jpn J Herpetol 15:1–21

Hikida T (2002) Natural history of the reptiles. University of Tokyo Press, Tokyo (in Japanese)

Hikida T (2003) Biogeography of reptiles in islands in East Asia: geographic distributions from views of molecular and morphological studies. Biol Sci (Tokyo) 54:205–220 (in Japanese)

Hikida T, Motokawa J (1999) Phylogeographical relationships of the skinks of the genus *Eumeces* (Reptilia: Scincidae) in East Asia. In: Ota H (ed) Tropical island herpetofauna: origin, current diversity, and conservation. Elsevier Science, Amsterdam, pp 231–247

Hikida T, Ota H (1997) Biogeography of reptiles in the subtropical East Asian islands. In: Lue KY, Chen T (eds) Proceedings of the symposium on the phylogeny, biogeography and conservation of fauna and flora of East Asian fegion. National Science Council, R.O.C., Taipei, pp 11–28

Hikida T, Ota H, Kuramoto M, Toyama M (1989) Zoogeography of amphibians and reptiles in East Asia. In: Matsui M, Hikida T, Goris RC (eds) Current herpetology in East Asia. Herpetological Society of Japan, Kyoto, pp 278–281

Hikida T, Ota H, Toyama M (1992) Herpetofauna of an encounter zone of Oriental and Palearctic elements: amphibians and reptiles of the Tokara Group and adjacent islands in the northern Ryukyus, Japan. Biol Mag (Okinawa) 30:29–43

Hirayama R (2001) Fossil turtles from the Tsubusagawa Formation (Pliocene) of Ajimu-cho, Oita Prefecture, Northern Kyushu, Japan. Res Rep Lake Biwa Mus Proj Office 18:79–96 (in Japanese with English abstract)

Hirayama R (2006) Review of fossil turtles of Japan. Fossils 80:47–59 (in Japanese with English abstract)

Hirayama R, Kaneko N, Okazaki H (2007) *Ocadia nipponica*, a new species of aquatic turtle (Testudines: Testudinoidea: Geoemydidae) from the Middle Pleistocene of Chiba Prefecture, central Japan. Paleontol Res 11(1):1–19

Honda M, Yasukawa Y, Hirayama R, Ota H (2002) Phylogenetic relationships of the Asian box turtles of the genus *Cuora* sensu lato (Reptilia: Bataguridae) inferred from mitochondrial DNA sequences. Zool Sci 19:1305–1312

Honda M, Kurita T, Toda M, Ota H (2014) Phylogenetic relationships, genetic divergence, historical biogeography and conservation of an endangered gecko, *Goniurosaurus kuroiwae* (Squamata: Eublepharidae), from the Central Ryukyus, Japan. Zool Sci 31:309–320

Ineich I (1999) Spatio-temporal analysis of the unisexual-bisexual *Lepidodactylus lugubris* complex (Reptilia, Gekkonidae). In: Ota H (ed) Tropical island herpetofauna: origin, current diversity, and conservation. Elsevier Science, Amsterdam, pp 199–228

Kizaki K, Oshiro I (1977) Paleogeography of the Ryukyu islands. Mar Sci Mon 9:542–549 (in Japanese with English abstract)

Koizumi Y, Ota H, Hikida T (2014) Phylogeography of the two smooth skinks, *Scincella boettgeri* and *S. formosensis* (Squamata: Scincidae) in the southern Ryukyus and Taiwan, as inferred from variation in mitochondrial cytochrome *b* sequences. Zool Sci 31:228–236

Kraus F (2009) Alien reptiles and amphibians: a scientific compendium and analysis. Springer, Berlin

Kurita K, Hikida T (2014a) Divergence and long-distance overseas dispersals of island populations of the Ryukyu five-lined skink, *Plestiodon marginatus* (Scincidae: Squamata), in the Ryukyu Archipelago, Japan, as revealed by mitochondrial DNA phylogeography. Zool Sci 31:187–194

Kurita K, Hikida T (2014b) A new species of *Plestiodon* (Squamata: Scincidae) from Kuchinoshima Island in the Tokara Group of the northern Ryukyus, Japan. Zool Sci 31:464–474

Kuriyama T, Brandley MC, Katayama A, Mori A, Honda M, Hasegawa M (2011) A time-calibrated phylogenetic approach to assessing the phylogeography, colonization history and phenotypic evolution of snakes in the Japanese Izu Islands. J Biogeogr 38:259–271

Lei J, Sun X, Jiang K, Vogel G, Booth DT, Ding L (2014) Multilocus phylogeny of *Lycodon* and the taxonomic revision of *Oligodon multizonatum*. Asian Herpetol Res 5(1):26–37

Lenk P, Fritz U, Joger U, Wink M (1999) Mitochondrial phylogeography of the European pond turtle, *Emys orbicularis* (Linnaeus 1758). Mol Ecol 8:1911–1922

Lin S, Chen CA, Lue K (2002) Molecular phylogeny and biogeography of the grass lizards genus *Takydromus* (Reptilia: Lacertidae) of East Asia. Mol Phylogenet Evol 22(2):276–288

Liu Q, Myers EA, Zhong GH, Hu J, Zhao H, Guo P (2012) Molecular evidence on the systematic position of the lance-headed pitviper *Protobothrops maolaneisis* Yang et al., 2011. Zootaxa 3178:57–62

Lue K, Lin S (2008) Two new cryptic species of *Takydromus* (Squamata: Lacertidae) from Taiwan. Herpetologica 64(3):379–395

Maenosono T, Toda M (2007) Distributions of amphibians and terrestrial reptiles in the Ryukyu archipelago: a review of published records. Akamata 18:28–46 (in Japanese)

Malhotra A, Thorpe RS (2000) The dynamics of natural selection and vicariance in the Dominican anole: patterns of within-island molecular and morphological divergence. Evolution 54 (1):245–258

Malhotra A, Thorpe RS (2004) Phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pitvipers (*Trimeresurus* and *Ovophis*). Mol Phylogenet Evol 32:83–100

Matsuo T (2005) Amphibians and reptiles in Nagasaki Prefecture. Nagasaki-shinbunsha, Nagasaki (in Japanese)

Motokawa J, Hikida T (2003) Genetic variation and differentiation in the Japanese five-lined skink, *Eumeces latiscutatus* (Reptilia: Squamata). Zool Sci 20:97–106

Nakamura Y, Takahashi A, Ota H (2014) A new, recently extinct subspecies of the Kuroiwa's leopard gecko, *Goniurosaurus kuroiwae* (Squamata: Eublepharidae), from Yoronjima Island of the Ryukyu Archipelago, Japan. Acta Herpetol 9(1):61–73

Okamoto T, Hikida T (2012) A new cryptic species allied to *Plestiodon japonicus* (Peters, 1864) (Squamata: Scincidae) from eastern Japan, and diagnoses of the new species and two parapatric congeners based on morphology and DNA barcode. Zootaxa 3436:1–23

Okamoto T, Motokawa J, Toda M, Hikida T (2006) Parapatric distribution of the lizards *Plestiodon* (formerly *Eumeces*) *latiscutatus* and *P. japonicus* (Reptilia: Scincidae) around the Izu Peninsula, central Japan, and its biogeographic implications. Zool Sci 23:419–425

Ota H (1998) Geographic pattern of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Res Popul Ecol 40:189–204

Ota H (2000) The current geographic faunal pattern of reptiles and amphibians of the Ryukyu Archipelago and adjacent regions. Tropics 10(1):51–62

Ota H (2003) A new subspecies of the agamid lizard, *Japalura polygonata* (Hallowell, 1861) (Reptilia: Squamata), from Yonagunijima Island of the Yaeyama Group, Ryukyu Archipelago. Curr Herpetol 22:61–71

Ota H, Iwanaga S (1997) A systematic review of the snakes allied to *Amphiesma pryeri* (Boulenger) (Squamata: Colubridae) in the Ryukyu Archipelago, Japan. Zool J Linn Soc 121:339–360

Ota H, Lin J, Chen S (1997) Systematic review of colubrid snakes of the genus *Pareas* in the East Asian islands. J Herpetol 31(1):79–87

Ota H, Ito A, Lin J (1999) Systematic review of the elapid snakes allied to *Hemibungarus japonicus* (Günther, 1868) in the East Asian islands, with description of a new subspecies from the central Ryukyus. J Herpetol 33(4):675–687

Ota H, Honda M, Chen S, Hikida T, Panha S, Oh H, Matsui M (2002) Phylogenetic relationships, taxonomy, character evolution and biogeography of the lacertid lizards of the genus *Takydromus* (Reptilia: Squamata): a molecular perspective. Biol J Linn Soc 76:493–509

Ota H, Toda M, Masunaga G, Kikukawa A, Toda M (2004) Feral populations of amphibians and reptiles in the Ryukyu Archipelago, Japan. Global Environ Res 8:133–143

Paik N, Min M, Shim J, Yang S, Toriba M (1993) Isozyme analysis of the species of the genus *Agkistrodon* in Far Eastern region. Snake 25:99–104

Poulakakis N, Lymberakis P, Tsigennopoulos CS, Magoulas A, Mylonas M (2005) Phylogenetic relationships and evolutionary history of snake-eyed skink *Ablepharus kitaibelii* (Sauria: Scincidae). Mol Phylogenet Evol 34:245–256

Rösler H, Bauer AM, Heinicke MP, Greenbaum E, Jackman T, Nguyen TQ, Zieagler T (2011) Phylogeny, taxonomy; and zoogeography of the genus *Gekko* Laurenti, 1768 with the revalidation of *G. reevesii* Gray, 1831 (Sauria: Gekkonidae). Zootaxa 2989:1–50

Sato H, Ota H (1999) False biogeographical pattern derived from artificial animal transportations: a case of the soft-shelled turtle, *Pelodiscus sinensis*, in the Ryukyu Archipelago, Japan. In: Ota H (ed) Tropical island herpetofauna: origin, current diversity, and conservation. Elsevier Science, Amsterdam, pp 317–334

Sengoku S, Hikida T, Matsui M, Nakaya K (eds) (1996) The encyclopedia of animals in Japan, volume 5: amphibians, reptiles, Chondrichthyes. Heibonsha, Tokyo (in Japanese)

Spinks PQ, Shaffer HB, Iverson JB, McCord WP (2004) Phylogenetic hypotheses for the turtle family Geoemydidae. Mol Phylogenet Evol 32:164–182

Surget-Groba Y, Heulin B, Guillaume C, Thorpe RS, Kupriyanova L, Vogrin N, Maslak R, Mazzotti S, Venczel M, Ghira I, Odierra G, Leontyeva O, Monney JC, Smith N (2001) Interspecific phylogeography of *Lacerta vivipara* and the evolution of viviparity. Mol Phylogenet Evol 18(3):449–459

Suzuki D, Hikida T (2014) Taxonomic status of the soft-shell turtle populations in Japan: a molecular approach. Curr Herpetol 33(2):171–179

Takahashi A, Kato T, Ota H (2007) A new species of the genus *Geoemyda* (Chelonii: Geoemydidae) from the Upper Pleistocene of Tokunoshima Island, the central Ryukyus, Japan. Curr Herpetol 26(1):1–11

Takahashi A, Otsuka H, Ota H (2008) Systematic review of Late Pleistocene turtles (Reptilia: Chelonii) from the Ryukyu Archipelago, Japan, with special reference to paleogeographical implications. Pac Sci 62(3):395–402

Takahashi A, Ōki K, Ishido T, Hirayama R (2013) A new species of the genus *Ocadia* (Testudines: Geoemydidae) from the middle Miocene of Tanegashima Island, southwestern Japan and its paleogeographic implications. Zootaxa 3647:527–540

Takahashi A, Otsuka H, Ota H (2015) A new species of the genus *Mauremys* (Testudines: Geoemydidae) from the Upper Pleistocene of Miyakojima Island, Ryukyus Archipelago, Japan. Curr Herpetol 34(2):149–163

Takeuchi H, Ota H, Oh H, Hikida T (2012) Extensive genetic divergence in the East Asian natricine snake, *Rhabdophis tigrinus* (Serpentes: Colubridae), with special reference to prominent geographical differentiation of the mitochondrial cytochrome *b* gene in Japanese populations. Biol J Linn Soc 105:395–408

Takeuchi H, Takeuchi M, Hikida T (2013) Extremely low genetic diversity in the Japanese population of *Zootoca vivipara* (Squamata: Lacertidae) revealed by mitochondrial DNA. Curr Herpetol 32:66–70

Takeuchi H, Zhu G, Ding L, Tang Y, Ota H, Mori A, Oh H, Hikida T (2014) Taxonomic validity and phylogeography of the east Eurasian natricine snake, *Rhabdophis lateralis* (Berthold,

1859) (Serpentes: Colubridae), as inferred from mitochondrial DNA sequence data. Curr Herpetol 32(2):148–153

Tang X, Chen Q (2006) On the taxonomic status of *Platyplacous sylvaticus* based on 12S rRNA gene. Acta Zootax Sin 31(3):475–479 (in Chinese with English abstract)

Toda M (2008) External characters useful to discriminate *Gekko hokouensis* and its cryptic undescribed species of the Okinawa Group, Japan: a preliminary report. Akamata 19:23–30 (in Japanese)

Toda M (2014) Ogasawara snake-eyed skink. In: Ministry of the Environment J (ed) Red Data Book 2014. Threatened wildlife of Japan, vol 3, Reptilia/Amphibia. GYOSEI Corporation, Tokyo, p 76 (in Japanese)

Toda M, Yoshida T (2005) Issues and perspectives regarding invasive alien species of amphibians and reptiles in Japan. Bull Herpetol Soc Jpn 2005(2):139–149 (in Japanese)

Toda M, Nishida M, Tu M, Hikida T, Ota H (1999) Genetic variation, phylogeny and biogeography of the pitvipers of the genus *Trimeresurus sensu lato* (Reptilia: Viperidae) in the subtropical East Asian islands. In: Ota H (ed) Tropical island herpetofauna: origin, current diversity, and conservation. Elsevier Science, Amsterdam, pp 249–270

Toda M, Hikida T, Ota H (2001) Discovery of sympatric cryptic species within *Gekko hokouensis* (Gekkonidae: Squamata) from the Okinawa Islands, Japan, by use of allozyme data. Zool Scr 30:1–11

Toda M, Sengoku S, Hikida T, Ota H (2008) Description of two new species of the genus *Gekko* (Squamata: Gekkonidae) from the Tokara and Amami Island Groups in the Ryukyu Archipelago, Japan. Copeia 2008:452–466

Tseng S, Wang C, Li S, Lin S (2015) Within-island speciation with an exceptional case of distinct separation between two sibling lizard species divided by a narrow stream. Mol Phylogenet Evol 90:164–175

Tu M, Wang H, Tsai M, Toda M, Lee W, Zhang F, Ota H (2000) Phylogeny, taxonomy, and biogeography of the Oriental pitvipers of the genus *Trimeresurus* (Reptilia: Viperidae: Crotalinae): a molecular perspective. Zool Sci 17:1147–1157

Turtle Taxonomy Working Group [van Dijk PP, Iverson JB, Rhodin AGJ, Shaffer HB, Bour R] (2014) Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. In: Rhodin AGJ, Pritchard PCH, van Dijk PP, Saumure RA, Buhlmann KA, Iverson JB, Mittermeier RA (eds) Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Res Monogr 5(7):000.329–479. http://www.iucn-tftsg.org/wp-content/uploads/file/Accounts/crm_5_000_checklist_v7_2014.pdf

Utiger U, Helfenberger N, Schätti B, Schmidt C, Ruf M, Ziswiler V (2002) Molecular systematics and phylogeny of old and new world ratsnakes, *Elaphe* Auct., and related genera (Reptilia, Squamata, Colubridae). Russ J Herpetol 9(2):105–124

Vogel G, David P, Pauwels OSG, Sumontha M, Norval G, Hendrix R, Vu NT, Ziegler T (2009) A revision of *Lycodon ruhstrati* (Fischer 1886) auctorum (Squamata Colubridae), with the description of a new species from Thailand and a new subspecies from the Asian mainland. Trop Zool 22:131–182

Wang Y, Jin M, Li Y, Grismer LL (2014) Description of a new species of *Goniurosaurus* (Squamata: Eublepharidae) from the Guangdong Province, China, based on molecular and morphological data. Herpetologica 70(3):309–322

Wüster W, Peppin L, Pook CE, Walker DE (2008) A nesting of vipers: phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). Mol Phylogenet Evol 49:445–459

Xiang G, Li P, Yang Y (2009) Amphibians and reptiles of Taiwan. Maotouying, Taipei (in Chinese)

Xu Y, Liu Q, Myers EA, Wang L, Huang S, He Y, Peng P, Guo P (2012) Molecular phylogeny of the genus *Gloydius* (Serpentes: Crotalinae). Asian Herpetol Res 3(2):127–132

Yamashiro S, Toda M, Ota H (2000) Clonal composition of the parthenogenetic gecko, *Lepidodactylus lugubris*, at the northernmost extremity of its range. Zool Sci 17:1013–1020

Zhang Y, Zhao K (1978) On the zoogeographical regions of China. Acta Zool Sin 24(2):196–202

Zhang B, Huang X, Pan T, Zhang L, Zhou W, Song T, Han D (2013) Systematics and species validity of the Dabieshan pit viper *Protobothrops dabieshanensis* Huang et al. 2012: evidence from a mitochondrial gene sequence analysis. Asian Herpetol Res 4(4):282–287

Zhao E, Adler K (1993) Herpetology of China. Society for the Study of Amphibians and Reptiles, Oxford

Chapter 6
Species Diversity of Japanese Amphibians: Recent Progress and Future Prospects of Systematic Studies

Kanto Nishikawa

Abstract A review of the systematic study of Japanese amphibians, especially focusing on recent taxonomic changes, phylogeographic study, conservation, and future prospects, is presented here. The number of known amphibian species and the degree of their endemism has been greatly revised, then increased, in Japan, especially in this decade. However, the systematic study of Japanese amphibians is far from complete and many new species are still waiting to be described. The recent development of genetic analysis has promoted the systematic study of Japanese amphibians. Presently, new analyses by the use of DNA reveal fine-scale, population- and species-level phylogeny and phylogeographic relationships in Japanese amphibians, and this trend will continue also in the next decade. The recent taxonomic changes urge us to modify conservation laws and the Red Data Book (RDB), a list of species that are endangered, at governmental and regional levels. For these purposes, we need more researchers majoring in the taxonomy, morphology, life history, and conservation of Japanese amphibians. To increase these numbers, we must train younger students engaged in such studies on amphibians.

Keywords Amphibia • Taxonomy • Species diversity • Morphology • Molecular phylogeny • Phylogeography • Conservation

6.1 Introduction

In Japan, two of the three extant orders of Amphibia, the orders Urodela (salamanders) and Anura (frogs), occur. Presently, Japanese amphibian species and subspecies number 76 according to the author's account, excluding 4 introduced species (Table 6.1). Among them, 1 species of salamander (*Salamandrella keyserlingii*) and 5 species of frogs (*Fejervarya kawamurai*, *Hyla japonica*, *Kurixalus eiffingeri*,

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Table 6.1 List of amphibian species from Japan

Anura Fischer von Waldheim, 1831
Bufonidae Gray, 1825
Bufo Laurenti, 1768
Bufo gargarizans Cantor, 1842
Bufo gargarizans miyakonis Okada, 1931
Bufo japonicus Temminck and Schlegel, 1838
Bufo japonicus formosus Boulenger, 1883
Bufo japonicus japonicus Temminck and Schlegel, 1838
Bufo torrenticola Matsui, 1976
Rhinella Fitzinger, 1826
Rhinella marina (Linnaeus, 1758)[a]
Dicroglossidae Anderson, 1871
Fejervarya Bolkay, 1915
Fejervarya kawamurai Djong, Matsui, Kuramoto, Nishioka and Sumida, 2011[b]
Fejervarya sakishimensis Matsui, Toda and Ota, 2007
Limnonectes Fitzinger, 1843
Limnonectes namiyei (Stejneger, 1901)
Hylidae Rafinesque, 1815
Hyla Laurenti, 1768
Hyla hallowellii Thompson, 1912
Hyla japonica Günther, 1859[b]
Microhylidae Günther, 1858
Microhyla Tschudi, 1838
Microhyla okinavensis Stejneger, 1901
Pipidae Gray, 1825
Xenopus Wagler, 1827
Xenopus laevis (Daudin, 1802)[a]
Ranidae Rafinesque, 1814
Babina Thompson, 1912
Babina holsti (Boulenger, 1892)
Babina subaspera (Barbour, 1908)
Glandirana Fei, Ye and Huang, 1990
Glandirana rugosa (Temminck and Schlegel, 1838)
Glandirana susurra (Sekiya, Miura and Ogata, 2012)
Lithobates Fitzinger, 1843
Lithobates catesbeianus (Shaw, 1802)[a]
Nidirana Dubois, 1992
Nidiana okinavana (Boettger, 1895)
Odorrana Fei, Ye and Huang, 1990
Odorrana amamiensis (Matsui, 1994)
Odorrana ishikawae (Stejneger, 1901)
Odorrana narina (Stejneger, 1901)
Odorrana splendida Kuramoto, Satou, Oumi, Kurabayashi and Sumida, 2011

(continued)

Table 6.1 (continued)

Odorrana supranarina (Matsui, 1994)
Odorrana utsunomiyaorum (Matsui, 1994)
Rana Linnaeus, 1758
Rana japonica Boulenger, 1879
Rana kobai Matsui, 2011
Rana neba Ryuzaki, Hasegawa and Kuramoto, 2014
Rana ornativentris Werner, 1903
Rana pirica Matsui, 1991[b]
Rana sakuraii Matsui and Matsui, 1990
Rana tagoi Okada, 1928
Rana tagoi tagoi Okada, 1928
Rana tagoi okiensis Daito, 1969
Rana tagoi yakushimensis Nakatani and Okada, 1966
Rana tsushimensis Stejneger, 1907
Rana uenoi Matsui, 2014
Rana ulma Matsui, 2011
Pelophylax Fitzinger, 1843
Pelophylax nigromaculatus (Hallowell, 1861)[b]
Pelophylax porosus (Cope, 1868)
Pelophylax porosus porosus (Cope, 1868)
Pelophylax porosus brevipodus (Ito, 1941)
Rhacophoridae Hoffman, 1932
Buergeria Tschudi, 1838
Buergeria buergeri (Temminck and Schlegel, 1838)
Buergeria japonica (Hallowell, 1861)
Kurixalus Ye, Fei and Dubois *in* Fei, 1999
Kurixalus eiffingeri (Boettger, 1895)[b]
Rhacophorus Kuhl and Van Hasselt, 1822
Rhacophorus arboreus (Okada and Kawano, 1924)
Rhacophorus owstoni (Stejneger, 1907)
Rhacophorus schlegelii (Günther, 1858)
Rhacophorus viridis (Hallowell, 1861)
Rhacophorus viridis viridis (Hallowell, 1861)
Rhacophorus viridis amamiensis Inger, 1947
Polypedates Tschudi, 1838
Polypedates leucomystax (Gravenhorst, 1829)[a]
Caudata Scopoli, 1777
Cryptobranchidae Fitzinger, 1826
Andrias Tschudi, 1837
Andrias japonicus (Temminck, 1836)
Hynobiidae Cope, 1860
Hynobius Tschudi, 1838
Hynobius abei Sato, 1934

(continued)

Table 6.1 (continued)

Hynobius amakusaensis Nishikawa and Matsui, 2014
Hynobius boulengeri (Thompson, 1912)
Hynobius dunni Tago, 1931
Hynobius hidamontanus Matsui, 1987
Hynobius hirosei Lantz, 1931
Hynobius katoi Matsui, Kokuryo, Misawa and Nishikawa, 2004
Hynobius kimurae Dunn, 1923
Hynobius lichenatus Boulenger, 1883
Hynobius naevius (Temminck and Schlegel, 1838)
Hynobius nebulosus (Temminck and Schlegel, 1838)
Hynobius nigrescens Stejneger, 1907
Hynobius okiensis Sato, 1940
Hynobius osumiensis Nishikawa and Matsui, 2014
Hynobius retardatus Dunn, 1923
Hynobius shinichisatoi Nishikawa and Matsui, 2014
Hynobius stejnegeri Dunn, 1923
Hynobius takedai Matsui and Miyazaki, 1984
Hynobius tokyoensis Tago, 1931
Hynobius tsuensis Abe, 1922
Hynobius yatsui Oyama, 1947
Onychodactylus Tschudi, 1838
Onychodactylus fuscus Yoshikawa and Matsui, 2014
Onychodactylus intermedius Yoshikawa and Matsui, 2014
Onychodactylus japonicus (Houttuyn, 1782)
Onychodactylus kinneburi Yoshikawa, Matsui, Tanabe and Okayama, 2013
Onychodactylus nipponoborealis Kuro-o, Poyarkov and Vieites, 2012, *in* Poyarkov, Che, Min, Kuro-o, Yan, Li and Iizuka
Onychodactylus tsukubaensis Yoshikawa and Matsui, 2013
Salamandrella Dybowski, 1870
Salamandrella keyserlingii Dybowski, 1870[b]
Salamandridae Goldfuss, 1820
Cynops Tschudi, 1838
Cynops ensicauda (Hallowell, 1861)
Cynops pyrrhogaster (Boie, 1826)
Echinotriton Nussbaum and Brodie, 1982
Echinotriton andersoni (Boulenger, 1892)

[a] Introduced
[b] Not endemic to Japan

Pelophylax nigromaculatus, *Rana pirica*) are also distributed outside Japan, but the remaining 70 species and subspecies (92.1 % of the total species) are endemic to Japan (I here treated *Glandirana rugosa* as a species endemic to Japan, although the species was introduced into Hawaii, USA). This relatively large number of taxa and high endemism make the Japanese territory as one of the richest amphibian faunas in East Asia.

After Stejneger's (1907) first monumental book on amphibians from Japan and adjacent regions, only Matsui (2000) reviewed the systematic study of Japanese amphibians. As predicted by Matsui (2000), the number of known amphibian species from Japan (and adjacent region) greatly increased since his article appeared, mainly because of the systematic studies that described some populations of wide-ranging species as new, independent species. It is safe to say that our understanding of the species diversity of Japanese amphibians improved well after the publication by Matsui (2000). In the present chapter, I briefly review the progress in systematic studies for these 15 years and also mention some new threats to Japanese amphibians.

6.2 Taxonomic Changes After 2000

The number of native amphibian species known from Japan has steadily increased from 1782 [*Onychodactylus japonicus* (Houttuyn, 1782)] until 2015 (Fig. 6.1). After Matsui's (2000) review, the total number of known species greatly increased by description of a total of 17 new species, which correspond to 22.4 % of 76 species now known from Japan (Fig. 6.2). From this count, the 4 introduced species *Rhinella marina*, *Lithobates catesbeianus*, *Polypedates leucomystax*, and *Xenopus laevis* are excluded. *Andrias davidianus* is also found from Japan, but breeding is not recorded, although it interbreeds with *A. japonicus* (see below). I thus do not treat this species as an introduced species. Among 17 species described after 2000,

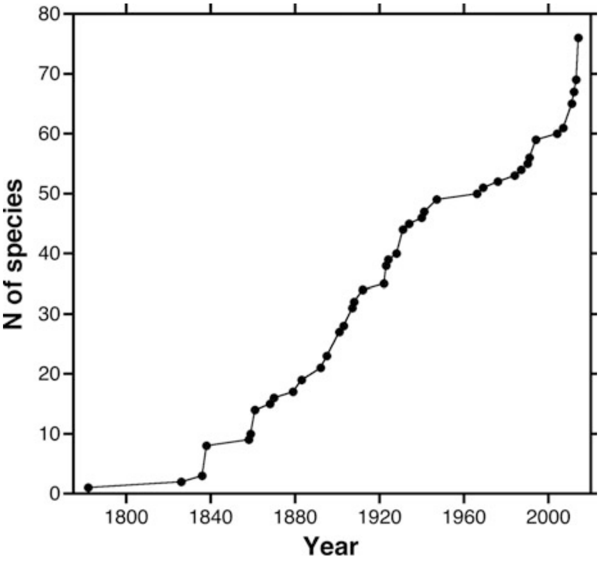

Fig. 6.1 Cumulative number of amphibian species recorded from Japan

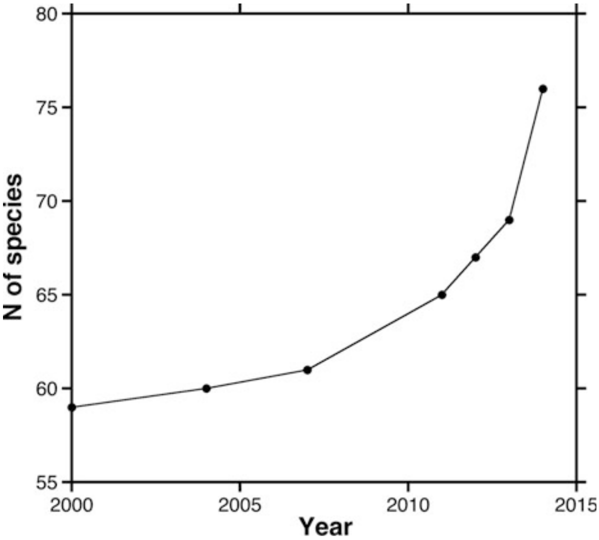

Fig. 6.2 Cumulative number of amphibian species recorded from Japan after 2000

only *Hynobius katoi* Matsui et al., 2004, *H. amakusaensis* Nishikawa and Matsui, 2014, *O. fuscus* Yoshikawa and Matsui, 2014, and *Glandirana susurra* (Sekiya et al., 2012) are newly discovered, and the others had been known as populations of the named species before their descriptions. Among the newly discovered species, only *G. susurra* is a frog, meaning that finding new frog species is quite difficult in Japan at present. The situation noted above means that the new species were mainly recognized by the examination of geographic variations of already known species: that is, *Fejervarya sakishimensis* Matsui et al., 2007 and *F. kawamurai* Djong et al., 2011, former *F. limnochari*; *H. osumiensis* Nishikawa and Matsui, 2014 and *H. shinichisatoi* Nishikawa and Matsui, 2014, former *H. boulengeri*; *O. nipponoborealis* Kuro-o et al., 2012, *O. tsukubaensis* Yoshikawa and Matsui, 2012, *O. kinneburi* Yoshikawa et al., 2013, and *O. intermedius* Yoshikawa and Matsui, 2014, former *O. japonicus*; *Rana neba* Ryuzaki et al., 2014, former *R. tagoi*; and *R. uenoi* Matsui, 2014, former *R. dybowskii*.

In this chapter, only the number of newly described species is taken into account. The number of synonymized species in a given period is quite small. Only *H. tenuis* was related to a junior synonym of *H. hidamontanus* by Matsui et al. (2002). *Rana kobai* Matsui, 2011 from Amami and *R. ulma* Matsui, 2011 from the Okinawa Islands were formerly known as a single species, *R. okinavana*, but the name proved to be preoccupied by *Nidirana psaltes* from Sakishima Islands (Matsui 2007). As the name *R. okinavana* was a replacement name of *N. psaltes*, the Amami and Okinawa populations of the former "*R. okinavana*" were described as two different new species.

It is noteworthy that a total of 15 species (88.2 % of the species described after 2000) have been described after 2011 (Fig. 6.2), including 8 urodelan and 7 anuran species, because the taxonomic studies of these taxa were conducted in this decade and that they came to be published in recent years.

6.3 Overview of Technical Change and Development

From the 1970s to recent times, electrophoretic studies on allozymes often have been conducted to assess taxonomic status and examine geographic variation of the Japanese amphibians (Matsui 2000). However, the number of electrophoretic studies is greatly decreased now. Studies on artificial hybridization and karyology, once often applied to taxonomic studies, also have greatly decreased and are rarely seen now. These electrophoretic, hybridization, and karyological data still offer usable information for systematic study and population genetics, but the recent great development of molecular techniques on DNA analysis has overwhelmed them. In contrast, acoustic analysis of mating calls still has been contributing well to recent taxonomic studies on frogs (Sekiya et al. 2012; Ryuzaki et al. 2014), because the analysis can document pre-isolating mechanisms for cryptic species in frogs.

From the 1990s, molecular techniques on mitochondrial DNA started to be applied for systematic and phylogeographic studies of Japanese amphibians (from Tanaka et al. 1996) and have replaced electrophoretic and other studies. After 2000, such studies mostly used mitochondrial DNA data and tended to increase the number of genes from the mitochondrial genome analyzed. Recently, studies based only on mitochondrial DNA tend to decrease because of criticism on the limited information from ‘single genome’ mitochondrial DNA, notwithstanding the increase of the number of genes analyzed. Instead, analyses of nuclear DNA became popular. However, available information from the nuclear genome tends to be much less variable, meaning ‘less informative for constructing a phylogenetic tree,’ than the mitochondrial one at present. Thus, many recent studies combine mitochondrial and nuclear DNA information to compensate for both disadvantages, or conduct microsatellite DNA analysis for population genetics.

In the next section, I introduce some of the recent systematic and phylogeographic studies on Japanese amphibians after 2000.

6.4 Recent Systematic and Phylogeographic Studies

6.4.1 Fire-Bellied Newts: Genus Cynops

Tominaga et al. (2010, 2013) examined geographic genetic variation in the Japanese fire-bellied newts, *Cynops ensicauda*, from the Central Ryukyus by use of mitochondrial DNA, and *C. pyrrhogaster* (Fig. 6.3) from mainland Honshu,

Fig. 6.3 A male of *Cynops pyrrhogaster* from the Chugoku District (Photograph courtesy of Mr. S. Ochi)

Shikoku, and Kyushu islands by use of mitochondrial and nuclear DNA sequences. Tominaga et al. (2010) found extensive genetic differentiation in *C. ensicauda* between the Okinawa and Amami Island groups, supporting the recognition by Inger (1947) of two subspecies, *C. e. ensicauda* (Amami Islands) and *C. e. popei* (Okinawa Islands), solely from morphological examination. From the degree of genetic differentiation, differences between these could be considered as a different specific level. Further, Tominaga et al. (2013) studied variation in *C. pyrrhogaster* and found that the northern populations (from Kanto to Tohoku regions of mainland Honshu) were consistently differentiated from the remaining populations of Japan from both mitochondrial and nuclear DNA analyses. Future morphological assessment is required at least for the northern populations. Tominaga et al. (2013) also showed by a population genetics analysis that glacial and postglacial oscillations might have caused population reductions and expansions in *C. pyrrhogaster*.

6.4.2 Indian Rice Frog: **Fejervarya limnocharis**

The populations of a frog long identified as *Fejervarya limnocharis* in Japan were separated into two new species, *F. sakishimensis* Matsui et al., 2007 in the Southern Ryukyus and *F. kawamurai* Djong et al., 2011 in mainland Honshu and Amami and Okinawa Island groups (also in central China and western Taiwan). Although the taxonomy of the former *F. limnocharis* was well revised within Japan, the taxonomic status of many populations of *F.* cf. *limnocharis* outside Japan still needs to be clarified. Toda (1999) reported that the populations from eastern Taiwan partly shared genetic characteristics with *F. sakishimensis*, suggesting gene flow between the two areas in the past. To decide the taxonomic status of the eastern Taiwan populations of *F.* cf. *limnocharis*, more samples from the area must be examined genetically. The populations from central China and western Taiwan were identified as *F. kawamurai* (Djong et al. 2011). However, Sumida et al. (2007) reported that the Okinawa Island populations (now *F. kawamurai*) formed a clade with

Fig. 6.4 A topotypic male of *Rana tagoi* from Gifu Prefecture (Photograph courtesy of Dr. K. Eto)

western Taiwan populations (*F. multistriata*), and not with the Honshu (*F. kawamurai*) or Southern Ryukyu populations (*F. sakishimensis*). The systematic relationships of *Fejervarya* spp. from Japan and adjacent areas are still far from completely understood (Kotaki et al. 2010).

6.4.3 Tago's Brown Frog: Rana tagoi

Rana tagoi (Fig. 6.4) is a unique brown frog with a subterranean breeding habit. The species occurs in mainland Honshu, Shikoku, Kyushu, and peripheral islands, and two island populations were separated as subspecies, *R. t. okiensis* and *R. t. yakushimensis*. It has been known that the species has a cryptic species syntopically distributed with the nominotypical subspecies *R. t. tagoi* in the Kinki region, mainland Honshu (Sugahara 1990; Sugahara and Matsui 1992). Eto and Matsui (2014) and Eto et al. (2012, 2013) conducted molecular phylogenetic and population genetic studies on *R. tagoi* and its close relative, *R. sakuraii*. They found more than ten lineages in *R. tagoi* and two in *R. sakuraii* in the mitochondrial phylogeny. Surprisingly, both of the two species, morphologically identified, were not monophyletic in the phylogeny. However, the relationship based on morphological information tended to be more similar to the relationship obtained by nuclear DNA than that by mitochondrial DNA, suggesting past introgressions among populations and species. Recently, Ryuzaki et al. (2014) described *R. neba* from central Honshu, mainly based on its peculiar chromosomal number of $2n = 28$ ($2n = 26$ in three subspecies of *R. tagoi*: Daito 1981; Maeda and Matsui 1999) and unique mating call. However, the species boundary of the new species is not clear. The entire taxonomic revision of this species complex is strongly required.

6.4.4 Odaigahara Salamander: Hynobius boulengeri

Nishikawa et al. (2001, 2005) recognized three genetically differentiated groups in *Hynobius boulengeri* and found, by allozyme analyses, that *H. stejnegeri*, endemic to the Kyushu Central Mountains, was nested in the Kyushu populations of *H. boulengeri*. On the basis of morphological and allozymic analyses on *H. boulengeri* and *H. stejnegeri*, Nishikawa et al. (2007) proposed to treat the population from the Kii Peninsula as *H. boulengeri* sensu stricto, that from Shikoku Island as *H. hirosei* Lantz, 1931, and the population from the Kyushu Central Mountains as *H. stejnegeri* Dunn, 1923. Finally, Nishikawa and Matsui (2014) described the remaining three Kyushu populations of *H. boulengeri* as new species—*H. amakusaensis*, *H. osumiensis*, and *H. shinichisatoi*—by adding mitochondrial DNA information. These authors also shed light on the relationships between external morphology of adult salamander and environmental variants, including the number of sympatric salamander species (Nishikawa et al. 2007), and the relationships among morphology, life history, and habitat in the larval stage (Nishikawa and Matsui 2008).

6.4.5 Wrinkled Frog: Glandirana rugosa

It has been known that Japanese populations of *Glandirana rugosa* showed great intraspecific variation in sex chromosomes (Miura 2007). Although the species possesses high variation in sex chromosomes, the morphological variation had not been well examined from a taxonomic aspect. Sekiya et al. (2012) newly found an enigmatic population of *G. rugosa* from Sado Island, which emitted a unique mating call and possessed external morphology different from *G. rugosa*, notably, a deep yellow belly and ventral hindlimbs (gray in *G. rugosa*). Based on these characteristics, Sekiya et al. (2012) described this population as a new species, *Rugosa susurra*, which is now moved to the genus *Glandirana* (Fig. 6.5). The discovery of *G. susurra* was totally unexpected. In Sado Island, *G. rugosa* also occurs parapatrically with *G. susurra*. Populations of *G. rugosa* from Sado Island and remaining areas in Japan with great variation in the sex chromosomes require to be taxonomically examined.

6.4.6 Ishikawa's Frog: Odorrana ishikawae

Odorrana ishikawae was a species endemic to the Okinawa and Amami Islands of the Ryukyu Archipelago. Kuramoto et al. (2011) conducted morphological and genetic comparisons and artificial hybridization experiments between the Amami and Okinawa Islands and found a critical difference between the two populations. Thus, they described the Amami populations as a new species, *O. splendida*

Fig. 6.5 A male *Glandirana susurra* from Niigata Prefecture (Photograph courtesy of Dr. K. Eto)

Fig. 6.6 A female *Odorrana splendida* from Kagoshima Prefecture (Photograph courtesy of Dr. A. Tominaga)

(Fig. 6.6). Igawa et al. (2013), members of the research group that described *O. splendida*, further examined intraspecific variation in *O. ishikawae* from Okinawa Island and *O. splendida* from Amami Island on a fine scale by use of microsatellite markers. By use of ecological niche modeling and landscape genetic analyses, they revealed the contrasting population structures of the two species to be caused by the degree of difference in topographical complexity between the two islands. Recently, Fei et al. (2010) proposed a new genus name, *Matsuirana*, for *O. ishikawae* (it should also include *O. splendida* now). If this taxonomy is accepted, this genus will be the first one endemic to Japan.

6.4.7 *Japanese Clawed Salamander:* Onychodactylus japonicus

Compared with the salamanders of the genus *Hynobius*, geographic study of intraspecific variation in the genus *Onychodactylus* was retarded (only *O. japonicus*

Fig. 6.7 A topotypic female of *Onychodactylus tsukubaensis* from Ibaraki Prefecture (Photograph courtesy of Dr. N. Yoshikawa)

had been known to occur in Japan). Yoshikawa et al. (2008, 2010a, b, 2012) first clarified the presence of cryptic species and sympatric distribution in several regions between different species pairs in *Onychodactylus*. However, after *O. nipponoborealis* was described by Poyarkov et al. (2012) from the northern Tohoku region, Yoshikawa and coworkers successively described new species: *O. tsukubaensis* (Fig. 6.7) from the Kanto region and *O. kinneburi* from Chugoku and Shikoku regions in 2013, and *O. intermedius* from southern Tohoku region and *O. fuscus* from a limited area in southern Tohoku region in 2014. The specific status of these taxa was determined mainly based on the combination of mitochondrial DNA and allozyme information provided by Yoshikawa et al. (2008, 2010a, b, 2012). The phylogeographic history of the species in the genus estimated by Yoshikawa et al. (2008) has been useful data for considering faunal formation in mainland Japan.

6.5 Conservation

Systematic study and conservation are closely associated. In Japan, many new species were described rapidly in these years. Some content in the conservation laws and the Red Data Books of the national and local governments still does not handle the up-to-date taxonomy. These governments need to consider modifying present laws or enforcing new laws. Recently, over-collection by pet traders and hobbyists, including foreigners, is becoming a great threat to the conservation of threatened species in Japan. Not only legal action but also conservational activity by local people is important to hamper such collections. Presently, conservation laws are being drafted for some new species, and their habitats are patrolled by volunteers.

Recent population genetic data have shown fine-scale geographic variation in Japanese amphibians (Igawa et al. 2013; Tominaga et al. 2010, 2013; Yoshikawa et al. 2008). Such information on regional genetic diversity will deter inconsiderate artificial transplantation of native threatened populations from the original habitats, that will be destroyed by development, to other areas. In that case, we must select candidate areas for the transplantation by considering genetic diversity. However, such transplant should be an inevitable choice only when we cannot conserve the original habitat, and should not be any kind of 'indulgence' (in the Catholic meaning) against destruction of the habitat.

Problems of invasive amphibian species into Japan have been recognized as much more serious than in the past decade. Introduction of the Chinese giant salamander, *Andrias davidianus*, into some prefectures in the Kinki area caused hybridization with the native *A. japonicus* and even backcrosses between the hybrids and native species. In the stream of the Kamo River in Kyoto Prefecture, 57 % of metamorphs and 71 % of larvae of the giant salamanders collected were confirmed as not pure Japanese species, but as Chinese species or hybrids (Matsui 2009). This disastrous situation was predicted and cautioned against when hundreds of Chinese giant salamanders were imported to Japan in the 1970s (Ikoma 1973).

Also, the introduced cane toad, *Rhinella marinus*, in the southern Ryukyus and the Ogasawara Islands, and the African clawed frog, *Xenopus laevis*, in some areas in Honshu Island, should be eliminated from nature as quickly as possible, before it is too late, as in the case of the already widespread *Lithobates catesbeianus* and *Polypedates leucomystax*, now impossible to exterminate from Japan. In the worst case, we are forced to give up attempting their extermination from an area when it is too late to do so.

We now should invest time and money for searching other areas where introduced species and/or hybrids are not found or rare, and must stop future invasion or stamp out these introductions at an earlier stage. To detect introduced species and hybrids of the giant salamander, recent work on e-DNA analysis developed by Fukumoto et al. (2015) could be a useful tool for estimating their relative abundance in a given river system. However, they developed their method based only on mitochondrial DNA markers, which can only detect maternal DNA and thus may fail to detect hybrids. The most immediately required issue is to develop a simple and quick method for genetic identification based on nuclear DNA analysis, one that can be done in the field, for effectively exterminating introduced and hybrid species from nature.

Because amphibians need wide habitats (both terrestrial and aquatic ones), and positions at the middle of the food chain in a given ecosystem, and as their high species diversity is very distinctive in the Japanese vertebrate fauna, it is initially a good index for conserving Japanese nature. As systematic study progresses, amphibians will be even more important index organisms for conserving nature in Japan.

6.6 Future Prospects

As introduced here, the taxonomic revisions of some taxa are far from complete and many new species await being described. Thus, it is certain that the number of amphibian species and their endemism will increase in Japan in the next decade.

Some wide-ranging species will be shown to include multiple cryptic species, mainly by use of genetic analysis, but their descriptions need considerable time for clarifying morphological distinctness. Recent genetic study also has shown that several species were genetically introgressed from conspecific populations and even from different species (see Sect. 6.4.3; e.g., *Rana tagoi*), whose taxonomic status will not be easily determined.

Information of new species for identification, not only for adults, but also for eggs, larvae, and juveniles, will be more important for inventory, ecological, behavioral, and conservational studies in Japanese amphibians. It is preferable to establish a standardized DNA barcoding system that can identify all Japanese species using tissues of any developmental stage. However, the large species number and great intraspecific variation will prohibit development of such a system by use of short sequences from a single gene, because it is not easy for all Japanese species to be separated by such limited information. We may need information from multiple genes or to develop a system that will be applicable only in a given area, and we must at least separate areas into mainland and the Ryukyus.

The appearance of next-generation sequencers is promoted to develop microsatellite markers, which will be a more common technique for systematic study on Japanese amphibians. The microsatellite data will contribute to parentage diagnosis and evaluation on individual fitness as associated with breeding strategy. Next-generation sequencers will also contribute to develop restriction site-associated DNA (RAD) analysis, which provides a new approach to non-model organisms without genomic information (Peterson et al. 2012; Takahashi et al. 2014). The RAD sequencing can be applied to conduct population- and species-level phylogenetic analyses and to develop simple sequence repeat (SSR) markers. Thus, the technique will be more widely applied to various studies on Japanese amphibians in the near future. The recent appearance of a portable sequencer may greatly change the inventory and field studies of amphibians in future (Hayden 2015).

As in the case of other organisms, the number of researchers engaged in morphological study is decreasing in the field of amphibian study in Japan. We cannot describe and identify species only by the genetic data. Even for developing a DNA barcoding system, reasonable taxonomy based on morphology is most important. Recent morphometric analyses such as the thin-plate spline method still have not been applied to Japanese amphibians. More morphological studies are required in Japanese amphibians.

Although there are many studies on conservational genetics, and on breeding technique and diseases in captivity, there are still few practical conservational studies applicable to wild populations and species. The chytridiomycosis caused by the chytrid fungus, *Batrachochytrium* spp., has not been a great threat against wild amphibian species in Japan, at least until now, because the disease is believed to be native to East Asian countries including Japan (Goka et al. 2009; Martel et al. 2014). In any case, a long-term study on ecological monitoring and accumulation on natural historical information of wild amphibians, and their successions to the next generations, are required. The succession of monitoring is critically important for some long-life amphibians, especially for the Japanese giant salamander, *Andrias japonicus*, which can live longer than 60 years.

6.7 Conclusion

In contrast to the recent great increase in the number of known species, the number of researchers on Japanese amphibians has not increased as much. Matsui (2000) proposed to save systematic batrachologists in East Asia, including Japan, from extinction, but the situation is not much improved yet in Japan. As already noted, amphibian study will be very important for the conservation of Japanese nature and wildlife. Many subjects that need to be studied and problems to be solved are left undone. We, thus, need to train younger students and present them with an interest in amphibian study in an attractive manner. The present article is also intended to achieve these purposes. Further, we need to establish and maintain laboratories for the interdisciplinary study of amphibians for a long time in more areas in Japan than are available in the present.

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References

Daito Y (1981) Karyotype of a new local population of *Rana tagoi yakushimensis*. Bull Fac Educ Kobe Univ 63:13–24

Djong TH, Matsui M, Kuramoto M et al (2011) A new species of the *Fejervarya limnocharis* complex from Japan (Anura, Dicroglossidae). Zool Sci 28:922–929

Eto K, Matsui M (2014) Cytonuclear discordance and historical demography of two brown frogs, *Rana tagoi* and *R. sakuraii* (Amphibia: Ranidae). Mol Phylogenet Evol 79:231–239

Eto K, Matsui M, Sugahara T et al (2012) Highly complex mitochondrial DNA genealogy in an endemic Japanese subterranean breeding Brown Frog *Rana tagoi* (Amphibia, Anura, Ranidae). Zool Sci 29:662–671

Eto K, Matsui M, Sugahara T (2013) Discordance between mitochondrial DNA genealogy and nuclear DNA genetic structure in the two morphotypes of *Rana tagoi tagoi* (Amphibia: Anura: Ranidae) in the Kinki Region, Japan. Zool Sci 30:553–558

Fei L, Ye CY, Jiang JP (2010) Phylogenetic systematics of Ranidae. Herpetol Sin 12:1–43

Fukumoto S, Ushimaru A, Minamoto T (2015) A basin-scale application of environmental DNA assessment for rare endemic species and closely related exotic species in rivers: a case study of giant salamanders in Japan. J Appl Ecol 52:358–365

Goka K, Yokoyama J, Une Y et al (2009) Amphibian chytridiomycosis in Japan: distribution, haplotypes, and possible route of entry into Japan. Mol Ecol 18:4757–4774

Hayden EC (2015) Pint-sized DNA sequencer impresses first users. Nature (Lond) 521:15–16

Igawa T, Oumi S, Katsuren S et al (2013) Population structure and landscape genetics of two endangered frog species of genus *Odorrana*: different scenarios on two islands. Heredity 110:46–56

Ikoma Y (1973) Collected works on the giant salamander (*Megalobatrachus japonicus*) in Japan. Tsuyama Museum of Science Education, Tsuyama

Inger RF (1947) Preliminary survey of the amphibians of the Riukiu islands. Fieldiana Zool 32:296–352

Kotaki M, Kurabayashi A, Matsui M et al (2010) Molecular phylogeny of the diversified frogs of genus *Fejervarya* (Anura: Dicroglossidae). Zool Sci 27:386–395

Kuramoto M, Satou N, Oumi S et al (2011) Inter- and intra-island divergence in *Odorrana ishikawae* (Anura, Ranidae) of the Ryukyu Archipelago of Japan, with description of a new species. Zootaxa 2767:25–40

Maeda N, Matsui M (1999) The frogs and toads of Japan. Revised edition. Tokyo: Bun-ichi Sogo Shuppan.

Martel A, Blooi M, Adriaensen C et al (2014) Recent introduction of a chytrid fungus endangers Western Palearctic salamanders. Science 346:630–631

Matsui M (2000) Batrachology of Japan and adjacent regions – a systematic review. Comp Biochem Physiol Part B 126:247–256

Matsui M (2007) Unmasking *Rana okinavana* Boettger, 1895 from the Ryukyus, Japan (Amphibia: Anura: Ranidae). Zool Sci 24:199–204

Matsui M (2009) Invasive alien species crisis. Shogakukan Inc, Tokyo

Matsui M (2014) Description of a new brown frog from Tsushima Island, Japan (Anura: Ranidae: *Rana*). Zool Sci 31:613–620

Matsui M, Nishikawa K, Misawa Y et al (2002) Taxonomic relationships of an endangered Japanese salamander *Hynobius hidamontanus* Matsui 1987 with *H. tenuis* Nambu 1991 (Amphibia: Caudata). Curr Herpetol 21:25–34

Miura I (2007) An evolutionary witness: the frog *Rana rugosa* underwent change of heterogametic sex from XY male to ZW female. Sex Dev 1:323–331

Nishikawa K, Matsui M (2008) A comparative study on the larval life history in two populations of *Hynobius boulengeri* from Kyushu, Japan (Amphibia: Urodela). Curr Herpetol 27:9–22

Nishikawa K, Matsui M (2014) Three new species of the salamander genus *Hynobius* (Amphibia, Urodela, Hynobiidae) from Kyushu, Japan. Zootaxa 3852:203–226

Nishikawa K, Matsui M, Tanabe S et al (2001) Geographic enzyme variation in a Japanese salamander, *Hynobius boulengeri* Thompson (Amphibia: Caudata). Herpetologica 57:281–294

Nishikawa K, Matsui M, Tanabe S (2005) Biochemical phylogenetics and historical biogeography of *Hynobius boulengeri* and *H. stejnegeri* (Amphibia: Caudata) from the Kyushu region, Japan. Herpetologica 61:54–62

Nishikawa K, Matsui M, Tanabe S et al (2007) Morphological and allozymic variation in *Hynobius boulengeri* and *H. stejnegeri* (Amphibia: Urodela: Hynobiidae). Zool Sci 24:752–766

Peterson BK, Weber JN, Kay EH et al (2012) Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping in model and non-model species. PLoS ONE 7:e37135

Poyarkov NA, Che J, Min M et al (2012) Review of the systematics, morphology and distribution of Asian clawed salamanders, genus *Onychodactylus* (Amphibia, Caudata: Hynobiidae), with the description of four new species. Zootaxa 3465:1–106

Ryuzaki M, Hasegawa Y, Kuramoto M (2014) A new brown frog of the genus *Rana* from Japan (Anura: Ranidae) revealed by cytological and bioacoustic studies. Alytes 31:49–58

Sekiya K, Miura I, Ogata M (2012) A new frog of the genus *Rugosa* from Sado Island, Japan (Anura, Ranidae). Zootaxa 3575:49–62

Stejneger L (1907) Herpetology of Japan and adjacent territory. Bull US Natl Mus 58:1–577

Sugahara T (1990) Reproductive ecology of *Rana tagoi tagoi* at Kitayama in Kyoto. Jpn J Herpetol 13:145

Sugahara T, Matsui M (1992) Larval growth and development in two types of the Japanese brown frog, *Rana tagoi tagoi*, at Kumogahata, Kyoto. Jpn J Herpetol 14:209

Sumida M, Kotaki M, Islam MM et al (2007) Evolutionary relationships and reproductive isolating mechanisms in the rice frog *Fejervarya limnocharis* complex from Sri Lanka, Thailand, Taiwan and Japan inferred from mtDNA gene sequence analysis, allozyme analysis and crossing experiments. Zool Sci 24:547–562

Takahashi T, Nagata N, Sota T (2014) Application of RAD-based phylogenetics to complex relationships among variously related taxa in a species flock. Mol Phylogenet Evol 80:137–144

Tanaka T, Matsui M, Takenaka O (1996) Phylogenetic relationships of Japanese brown frogs (*Rana*: Ranidae) assessed by mitochondrial cytochrome *b* gene sequences. Biochem Syst Ecol 24:299–307

Toda M (1999) Historical biogeography of East Asian populations of *Rana limnocharis* (Amphibia: Anura): a review. In: Ota H (ed) Tropical island herpetofauna: origin, current diversity, and conservation. Elsevier, Amsterdam, pp 299–315

Tominaga A, Ota H, Matsui M (2010) Phylogeny and phylogeography of the sword-tailed newt, *Cynops ensicauda* (Amphibia: Caudata), as revealed by nucleotide sequences of mitochondrial DNA. Mol Phylogenet Evol 54:910–921

Tominaga A, Matsui M, Yoshikawa N et al (2013) Phylogeny and historical demography of *Cynops pyrrhogaster* (Amphibia: Urodela): implication of taxonomic relationships and transitions of the distributional ranges associated with climate oscillations. Mol Phylogenet Evol 66:654–667

Yoshikawa N, Matsui M, Nishikawa K et al (2008) Phylogenetic relationships and biogeography of the Japanese clawed salamander, *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae), and its congener inferred from the mitochondrial cytochrome *b* gene. Mol Phylogenet Evol 49:249–259

Yoshikawa N, Matsui M, Nishikawa K et al (2010a) Allozymic variation of the Japanese clawed salamander, *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae), with special reference to the presence of two sympatric genetic types. Zool Sci 27:33–40

Yoshikawa N, Matsui M, Nishikawa K (2010b) Allozymic variation and phylogeography of two sympatric genetic types of *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae) in Kinki District, Japan. Zool Sci 27:344–355

Yoshikawa N, Matsui M, Nishikawa K (2012) Genetic structure and cryptic diversity of *Onychodactylus japonicus* (Amphibia, Caudata, Hynobiidae) in northeastern Honshu, Japan, as revealed by allozymic analysis. Zool Sci 29:229–237

Chapter 7
Japanese Freshwater Fishes: Biogeography and Cryptic Diversity

Katsutoshi Watanabe, Koji Tominaga, Jun Nakajima, Ryo Kakioka, and Ryoichi Tabata

Abstract More than 300 species of freshwater fishes are present in Japan. Because their distribution is expected to reflect geological history consequent to their low dispersal ability, they are a suitable group for studying historical relationships between land and biota. The strictly freshwater fish fauna in the Japanese Archipelago is primarily separated into two groups: those in northeastern Hokkaido, and those in other southwestern areas. The latter is further divided into two endemic faunas in the eastern and western regions across the Fossa Magna area. Recent phylogenetic and phylogeographic studies, primarily using mitochondrial DNA markers, support the importance of the Fossa Magana area in isolating related forms or intraspecific populations since the Late Miocene–Pliocene. This isolation, however, is not a primary one in some species. In western Japan, which has a rich and endemic freshwater fish fauna, both similar and different phylogeographic patterns have been observed among species, which may reflect differences in distribution histories and ecological traits of species. Further analyses using nuclear DNA loci, or genomic data, are necessary to elucidate the true processes of distribution, demography, and adaptation. Currently, 181 species/subspecies that depend heavily on freshwater environments are recognized in the Japanese Archipelago, but at least 244 evolutionary units (i.e., deep lineages with a long, unique history) are included in its freshwater fish fauna. The introduction of nonindigenous species is the primary driver for the decrease in β-diversity among regions, but the

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effects of species transplanted from other regions within Japan (i.e., the mixture and loss of endemic evolutionary units) remain underevaluated. Evolutionarily distinct units of freshwater fishes are historical legacies and should be maximally protected and passed on to future generations.

Keywords Area cladogram • Fossa Magna • Freshwater fish • mtDNA • Parsimony analysis of endemicity (PAE) • Phylogeography • Population structure

7.1 Introduction

The Japanese Archipelago is an island system extending more than 2000 km in a northeast–southwest direction on the eastern margin of East Asia. The repeated connection and disconnection of the archipelago with the continent of Asia and the development of mountainous topography likely influenced the development of the unique biota of the archipelago. The freshwater fish are a typical group whose distribution has been severely affected by geographic barriers, such as seas and mountains. Freshwater fish are often divided into three categories: primary (or strictly) freshwater fish, which are intolerant of saltwater and live only in freshwater for their entire life cycle; secondary freshwater fish, which have some salt tolerance and are occasionally able to cross narrow sea barriers; and peripheral freshwater fish, which are derived from marine ancestors and include the diadromous fish, migrating between fresh and marine environments (e.g., Myers 1949; Berra 2001; Lévêque et al. 2008; but also see Goto 1987). Geographic barriers specifically restrict the dispersal of primary freshwater fish; thus, they have been intensively studied in a biogeographic context (Darlington 1957; Lindberg 1972; Avise et al. 1987; Bănărescu 1990). Several studies of the freshwater fish fauna of Japan and adjacent areas have been performed following earlier descriptive biogeographical analyses (i.e., the classification of biogeographic regions) (Mori 1936; Taranetz 1936; Aoyagi 1957) (Fig. 7.1a).

About 300 freshwater fishes (including about 100 strictly freshwater species) are found in Japan, including the Japanese and Ryukyu Archipelagos (Kawanabe et al. 2001). Lindberg (1972) and Nishimura (1974) emphasized the multilayered nature of the Japanese freshwater fish fauna. They hypothesized that this was the result of repeated connections and separations between continental and Japanese freshwater systems caused by tectonic movement and sea level fluctuations during the Plio–Pleistocene (Fig. 7.1b). Although this idea was historically widely accepted (see Mizuno 1987), recent paleontological and phylogeographic studies have challenged the earlier hypothesis, specifically the fundamental assumptions of the time scales, pushing the events earlier (Watanabe et al. 2006; Watanabe and Takahashi 2010). The processes of the distribution of freshwater fishes should be examined using the contemporary approaches of historical biogeography.

In this chapter, we first reanalyze the faunal data for strictly freshwater fishes in the Japanese Archipelago, based on the analysis of Watanabe (2012). Then,

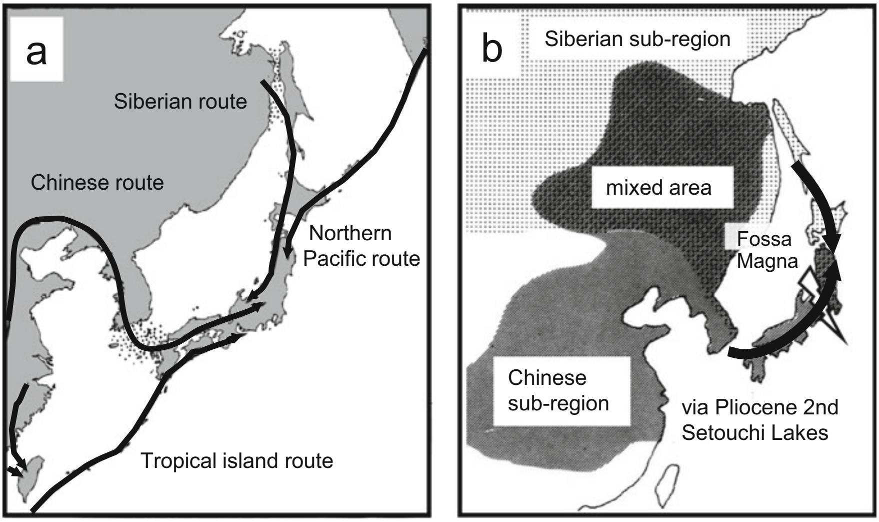

Fig. 7.1 Hypotheses for the formation and structure of the Japanese freshwater fish fauna. (**a**) The Aoyagi (1957) hypothesis of colonization routes during the glacial period. (**b**) The Nishimura (1974) hypothesis of distributional regions of East Asian freshwater fishes and dispersal routes in the Plio-Pleistocene. (After Watanabe 2012)

similarities and differences in geographic isolation patterns among species are examined by comparing the phylogeographic patterns of several widely distributed species with each other, as well as with the faunal structure. Based on these comparisons, we discuss the history of the freshwater fish fauna, focusing on the historical processes shaping the distribution of a representative species group along a time series. Summarizing recent phylogeographic studies, we also estimate the cryptic species diversity of the freshwater fishes, which has not yet been fully described. Finally, an outcome of artificial disturbance of the freshwater fish fauna is discussed, referring to the analysis of Watanabe (2012).

7.2 Faunal Structure of Freshwater Fishes

Using a presence/absence matrix of 93 strictly freshwater fish forms (native species, subspecies, and parts of distinct intraspecific monophyletic groups detected by genetic studies) from 27 regions of the Japanese Archipelago, Watanabe (2012) presented a hierarchical structure of the freshwater fish fauna as an area cladogram created using parsimony analysis of endemicity (PAE) (Rosen 1988; Brooks and van Veller 2003). The PAE area cladogram and an unweighted pair-group method with arithmetic mean (UPGMA) dendrogram based on Jaccard's distance (proportion of shared species between two areas) are compared in Fig. 7.2 (see Appendix 1 for the methods and data).

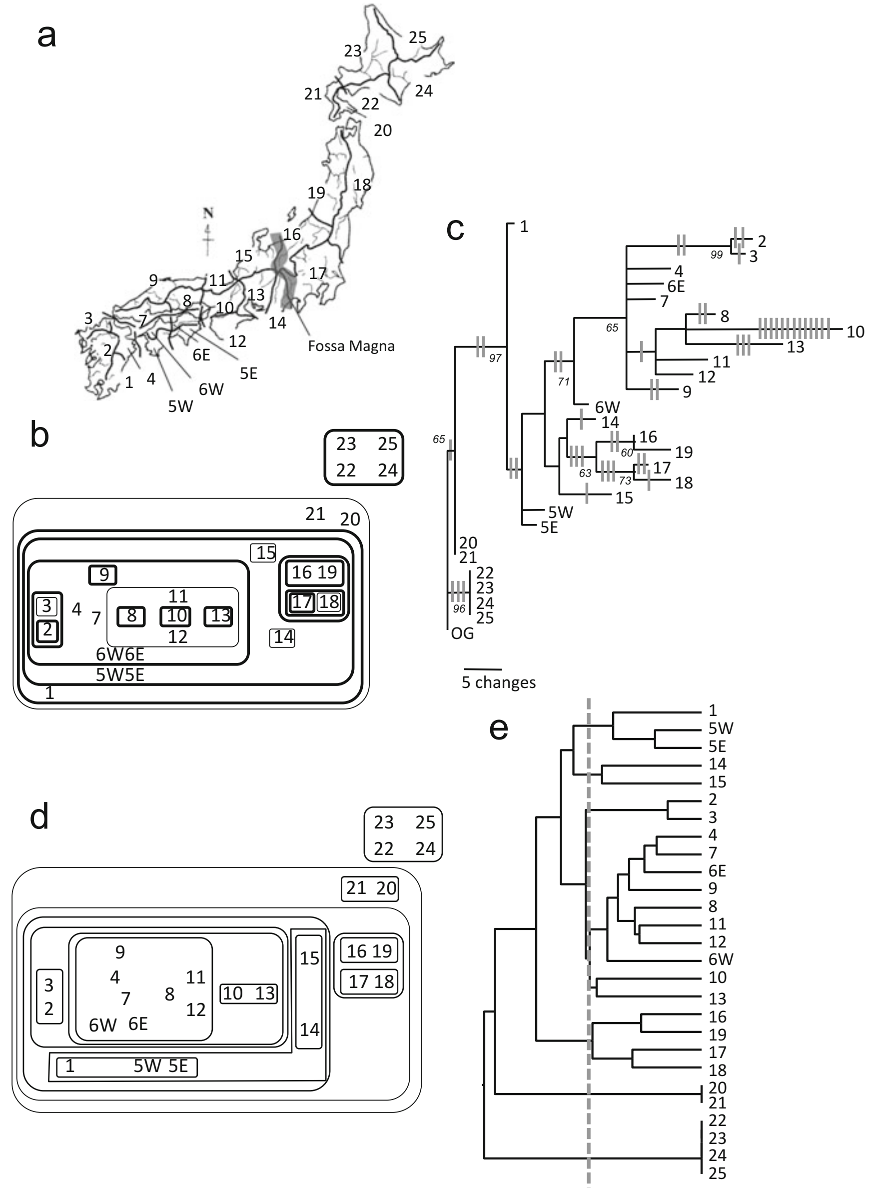

Fig. 7.2 (**a**) Regional division of the main islands of Japan for the faunal analysis of freshwater fishes. (**b**) Nested structure of endemic areas and strict consensus area cladogram calculated (**c**) using parsimony analysis of endemicity (PAE) for the distribution data of Japanese freshwater fishes (93 forms in 27 areas) (after Watanabe 2012). (**d**) Nested structure of areas and similarity relationships (**e**) among areas calculated by UPGMA using Jaccard's distances for the same data set. (Refer to Appendix 1 for the methods and area codes.) *Each vertical bar on a branch* in **c** represents an "apomorphic" (=endemic) fish form with CI = 1.0, according to the DELTRAN reconstruction. *Italicized numerals* represent the bootstrap probability (>50 %) for each branch.

The PAE area cladogram (strict consensus tree) contains 20 endemic areas defined by one or more endemic forms with a consistency index (CI) = 1.0 and 14 endemic areas defined by two or more such forms (Fig. 7.2b, c; see Watanabe 2012 for details). The cladogram successfully represents the relationships among regional faunas as recognized in the previous literature (Nishimura 1974). Specifically, the fauna of northeastern Hokkaido (areas 22–25) is first separated from the fauna in other southwestern areas (1–21) and the latter includes groups from two large endemic areas in the eastern (16–19) and western regions (2–4, 6W, 6E, 7–13) across the Fossa Magna area. The Fossa Magna was originally a channel running north to south crossing the center of Honshu Island, separating the southwestern and northeastern landmasses during the initial stage of the archipelago in the Middle Miocene (Kato 1992; Yonekura et al. 2001). A subsequent uplifting of the surrounding land has led to the formation of the great mountain ranges known as the Central Highlands and served as an important dispersal barrier for freshwater fishes in Japan. The western regions further include fauna from the cores of two endemic areas, that is, the eastern part of western Japan (Lake Biwa and adjacent areas; 8, 10–13) and northeastern Kyushu (2–3). The endemicity of the Lake Biwa–Yodo River system (included in area 10) is emphasized by 13 "autapomorphic" forms.

The UPGMA dendrogram pattern based on Jaccard's similarity of regional faunas is similar to the PAE cladogram, but an "absence" of taxa also characterizes some area groups (Fig. 7.2d, e). For example, peripheral areas of western Japan (areas 1, 5W, 5E, 14, and 15) are grouped because of a lack of several species commonly occurring in other areas of western Japan.

PAE cladograms are useful for characterizing an area or an area group because those areas can be defined by specific endemic taxa, and at least in some cases the presence of those taxa may imply biogeographic history shared between the areas with the assumptions that dispersal has not obliterated preceding vicariance patterns and that extinctions are random (Morrone and Crisci 1995; Watanabe 1998). In contrast, the absence of taxa in an area or an area group can reflect either local extinction or limited dispersal and colonization. Both are important in the distribution and formation of regional faunas (Ronquist 1997; Avise 2000). A regional fauna is an integrated consequence of many biogeographic and ecological events, and no single method will completely reveal the faunal structure.

Previous analyses have indicated the high endemicity of the Japanese freshwater fish fauna (Lindberg 1972; figs. 4 and 5 in Watanabe 2012). However, the structure and formation of the freshwater fish fauna of the Japanese Archipelago is complex, presumably because of the repeated connection and disconnection of the archipelago with the continent of Asia, as well as the lack of interruption by glaciation or complete marine submergence since the Late Miocene. Integration of phylogenetic

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Fig. 7.2 (continued) OG operational outgroup. *Solid and thin surrounding area*(*s*) in **b** indicate endemic areas defined by one and more than one endemic fish form, respectively. *A dashed line* in **e** is an arbitrary threshold for clustering areas and phylogeographic analyses for individual fish groups is necessary for further understanding of the history of the fauna.

7.3 Phylogeographic Structures and Distribution Processes

Since the 1970s, more than 500 papers have been published on the phylogeny, phylogeography, and related fields using molecular genetic markers of Japanese freshwater fishes (retrieved from the GEDIMAP database in August 2015; http://gedimap.zool.kyoto-u.ac.jp; Watanabe et al. 2010a). Early studies investigated protein (allozyme) polymorphisms, but since the late 1990s studies using mitochondrial DNA sequence data have been common (Appendix 2). In recent years, nuclear DNA sequences and microsatellites have been increasingly used in phylogenetic and population studies, respectively.

Considering the fundamentally low dispersal ability of strictly freshwater fishes, widely distributed species provide an excellent opportunity to infer the distribution and formation pattern of the biotas, because they may retain many historical signatures in their phylogeographic patterns. However, studies that reveal the full picture of phylogeographic patterns for the entire distribution ranges of species (or closely related species groups) are still limited. Well-analyzed representative groups of strictly freshwater fishes with full geographic sampling include several cyprinids, balitorids, and catfishes (Figs. 7.3 and 7.4 for representative examples): these exhibit both similar and different spatiotemporal patterns.

Associated with the Fossa Magna, or the Central Highlands area, vicariant pairs are found in several species groups (e.g., *Pseudorasbora pumila* and *P. pugnax*, *Acheilognathus typus* and *A. longipinnis*, and groups B and C of the *Pseudogobio esocinus* complex; Fig. 7.3), suggesting the primary role of this geographic barrier in their population divergence, as well as in the faunal structure (Fig. 7.2). In some species groups, the barrier seems to have had an important effect, but was not the primary influence (e.g., *Acheilognathus tabira* subsp., *Lefua echigonia*, and *Liobagrus reinii*; Fig. 7.3). Even including such groups, however, the population divergences associated with the Fossa Magna are deep, estimated to have occurred in the Late Miocene to the early Pleistocene in the species groups for which the divergence time was estimated (Fig. 7.3) (but also note that in some cases the divergence associated with the Fossa Magna itself was used as a lax constraint for the estimation purposes).

Similar and different spatiotemporal patterns have been also revealed for western Japan, which includes core areas with rich fish faunas (Fig. 7.4). Focusing on primary divergence, two major patterns are recognized, with the westernmost (areas 1–4) or easternmost areas (areas 13 and 14) involved in the basal divergences. The former includes species such as *Hemigrammocypris rasborella* (Fig. 7.4c) and *Squalidus gracilis* (Watanabe et al., unpublished data), and the latter includes *Biwia zezera* and *Sarcocheilichthys* spp. (Fig. 7.4e, g). Geologically, the isolation of the former areas by the Kanmon Straits (between Honshu and Kyushu) or the

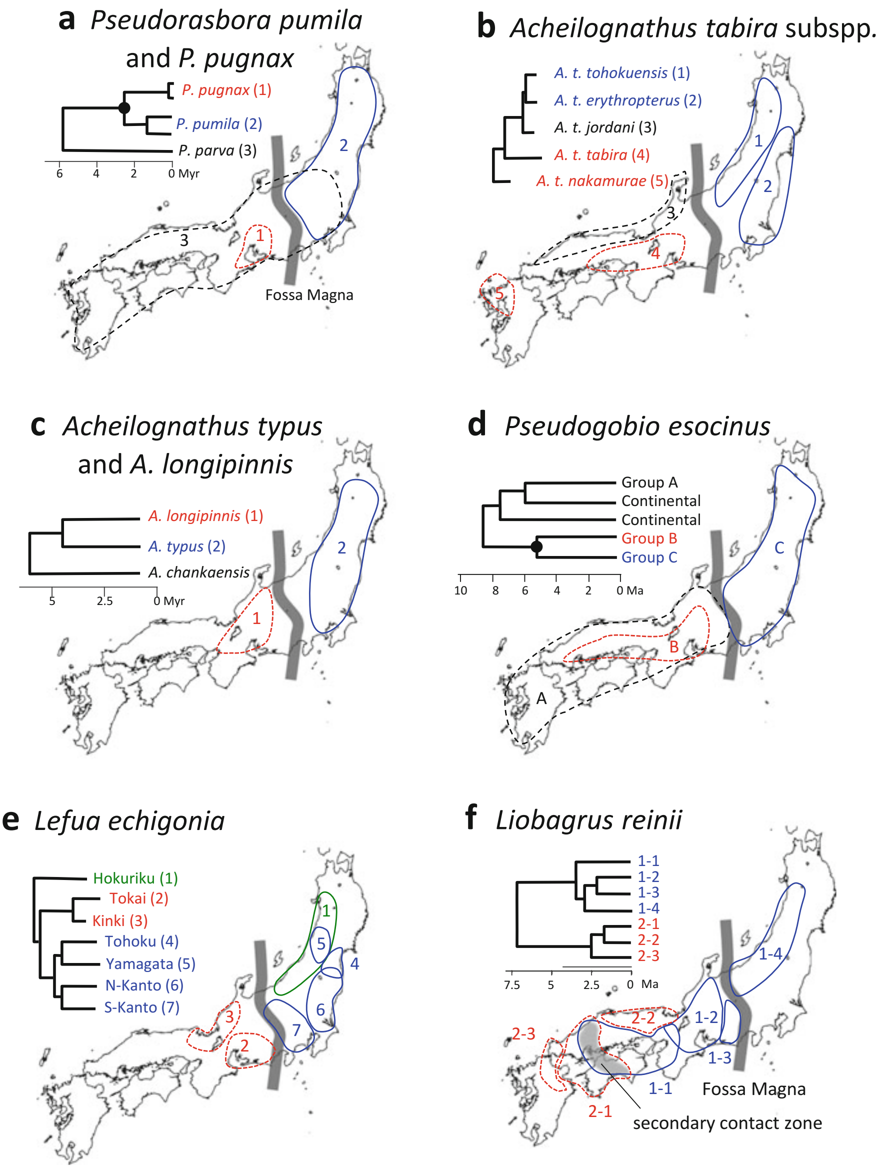


Fig. 7.3 Inter- and intraspecific vicariance patterns associated with the Fossa Magna area, or the Central Highlands, for six selected fish groups. Dated or not-dated phylogenetic trees were simply redrawn from original articles. *Black dots in the trees* represent calibration points for dating when used. *A gray line* shows the western edge of the Fossa Magna. (Modified from (**a**) Kakioka et al. (2013), (**b**) Kitamura et al. (2012), (**c**) Cheng et al. (2014), **d** Tominaga et al. (2016), (**e**) Miyazaki et al. (2011), (**f**) Nakagawa et al. (2016). See Appendix 4 for the references)

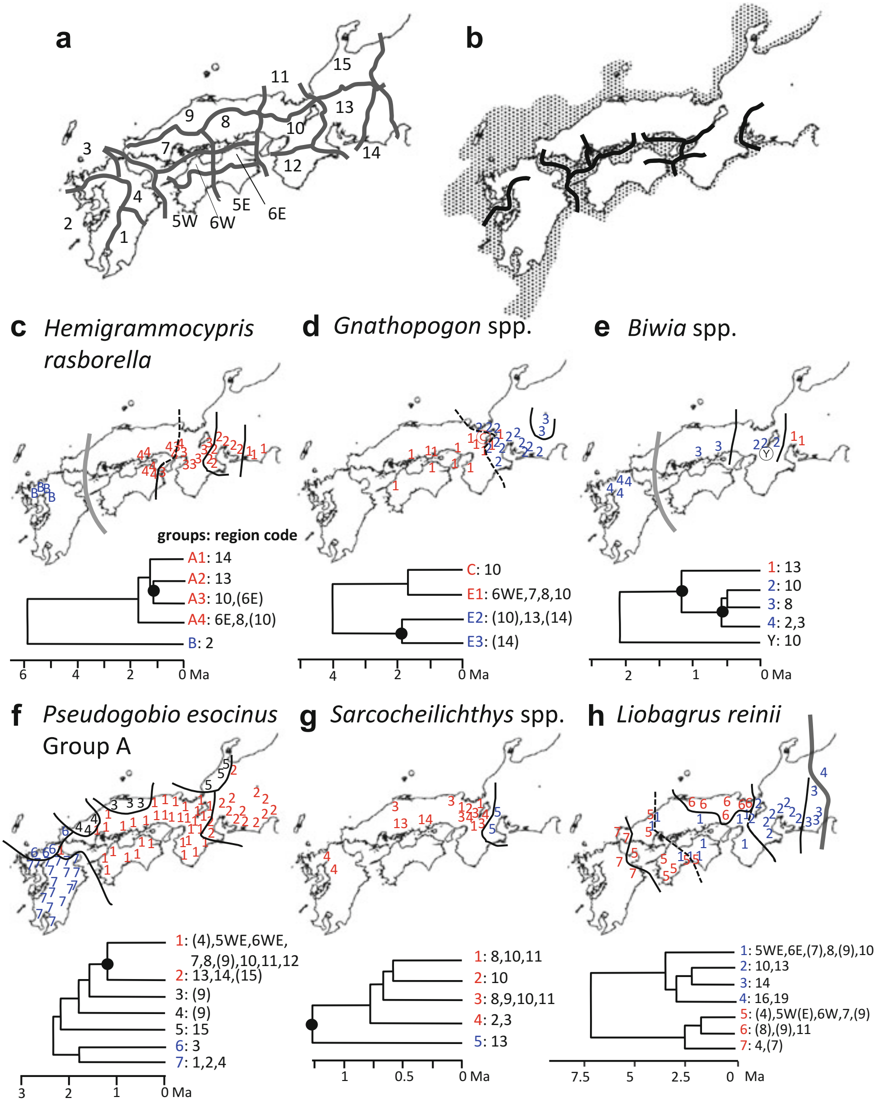


Fig. 7.4 (**a**) Regional divisions in western Japan. (**b**) Paleo-river systems (*thick lines*) and emerged areas (*shaded*) during the regression period (i.e., the Last Glacial Maximum, with sea level −200 m). (**c–f**) Regional population differentiations for six selected species groups. Dated trees were simply redrawn from original articles. *Black dots in the trees* represent calibration points for dating. (Modified from (**c**) Watanabe et al. (2014), (**d**) Kakioka et al. (2013), (**e**) Watanabe et al. (2010b), Watanabe (2013), (**f**) Tominaga et al. (2016), (**g**) Komiya et al. (2014), (**h**) Nakagawa et al. (2016). See Appendix 4 for the references)

Sangun–Hikosan Mountain systems in northern Kyushu occurred more recently [0.4–0.5 million years ago (MA) or later; Machida et al. 2006; Nakajima et al. 2006] than that of the latter areas, which have been separated from the western areas by the uplifting of the Suzuka Mountains since the early Pleistocene (1.0–1.5 MA; Yokoyama 1988; Kawabe 1994). Based on this chronological order of the geological barriers, the westernmost populations would be expected to have diverged later. Therefore, the highly differentiated populations in the westernmost area suggest that they diverged in association with earlier geological events (or for other reasons) and have remained in or colonized the area. The divergence across the Suzuka Mountains is obvious and common among most species, with a few exceptions (e.g., the cyprinid *Pungtungia herzi* and *Hemibarbus longirostris*, which have penetrated east to the Suzuka Mountains without distinct differentiation; Watanabe et al. unpublished data).

The area around the Seto Inland Sea, the core area of western Japan, emerged above the sea during glacial (regression) periods, and two major paleo-river systems—one flowing westward and another flowing eastward—appeared in this area (Fig. 7.4b) (Yonekura et al. 2001). Some species show distribution and population structure patterns likely corresponding to these paleo-river systems (e.g., *Liobagrus reinii*, Fig. 7.4h; the goby *Odontobutis obscura*, Sakai et al. 1998). However, this appears to be uncommon, and some level of gene flow might be present around the Seto Inland Sea (e.g., Fig. 7.4f, g). Lake Biwa, located at the easternmost end of the Seto Inland Sea area, would have been an important area not only as a center of origin for endemic species, but also as a refugium (or reservoir) for species and genetic diversity in western Japan (Watanabe 2013; Komiya et al. 2014), because it is the only large freshwater body that has existed since at least the middle Pleistocene (~0.4 MA) and is connected directly or indirectly with river systems around the Seto Inland Sea area (Watanabe 2013; Tabata et al. 2016).

The reasons for the interspecific differences in population structures are not well understood. Very deep divergences within species (e.g., *Hemigrammocypris rasborella* and *Liobagrus reinii*; Fig. 7.3), estimated to date back to the early Pliocene to the Miocene, should be distinguished from other more recent divergences. The uncertainty and misapplication of molecular dating should also be taken into consideration. Furthermore, phylogeographic analysis solely using mtDNA markers should be interpreted cautiously (Ballard and Whitlock 2004; Rubinoff and Holland 2005). The co-occurrence and mosaic distribution of differentiated mtDNA lineages in some species (Fig. 7.4) strongly suggest gene flow and replacement in parts of some regions (i.e., secondary contact or hybrid zones). In situations with incomplete geographic isolation, gene flow can be over- or underestimated by mtDNA information, and consequently the boundaries between regional populations and the position of hybrid zones inferred from mtDNA markers would not necessarily reflect the true population history. Repeated sea level fluctuations may not have completely geographically isolated freshwater fishes, and different population structure patterns could form based on the species dispersal ability, effective population size, and other ecological traits, as well as interspecific interactions and chance. Beyond enumeration and simple comparisons of the patterns, development of comparative phylogeographic approaches using nuclear DNA information with a broad range of variability (or genomic data) is necessary to understand the true histories of species and faunal formation involving dispersal, isolation, gene flow, and adaptation (Emerson et al. 2010; Davey et al. 2011; McCormack et al. 2013).

Phylogenetic and phylogeographic analyses of the gudgeon *Pseudogobio esocinus* species complex provide important insights into the dynamic formation processes of the Japanese freshwater fauna. Although most phylogeographic studies of widely distributed fishes have been limited to Japanese populations (or to species endemic to Japan), Tominaga et al. (2016) analyzed the data for fully sampled Japanese populations (from 200 localities) with those for continental populations of congeners presented by Xia et al. (2005). Using the mtDNA cytochrome *b* gene (and partly nuclear DNA gene) sequences, three distinct geographic groups (groups A, B, and C) were revealed. Groups B and C were found to be vicariants across the Fossa Magna region, as already mentioned (Fig. 7.3d). The estimation of divergence times suggest that groups B and C were older colonizers that had already expanded widely across Japan during the Early Pliocene, with differentiation associated with the uplift of the Central Highlands (Fig. 7.5). In contrast, group A split from a continental lineage in the Early Pliocene or Late Miocene, but has spread over western Japan since the Late Pliocene or later (after the uplifting of the Central Highlands). Another widely distributed freshwater fish group, the *Cobitis biwae* complex, shows a similar pattern in which old lineages have remained in eastern Japan and a part of western Japan, with a newer lineage having a wide range in western Japan (Kitagawa et al. 2003). These examples demonstrate the multilayered formation processes of the Japanese freshwater fish fauna related to the complex geographic history of the Japanese Archipelago and the continental area.

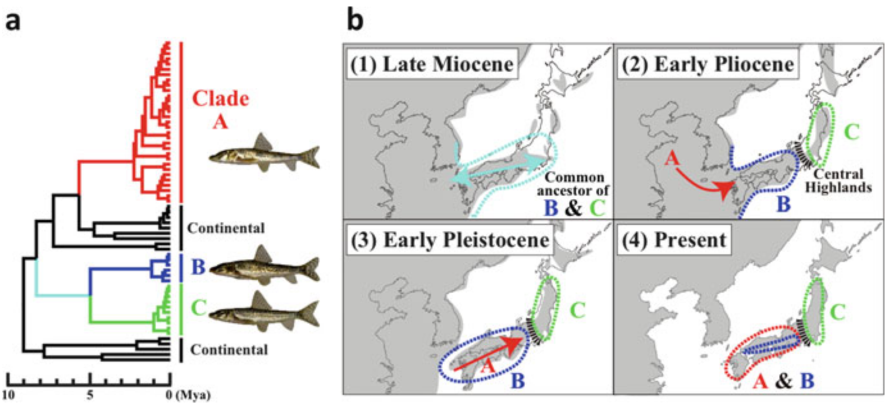


Fig. 7.5 (**a**) mtDNA phylogeny of the gudgeon *Pseudogobio esocinus* with continental relatives. (**b**) Schematic figures of the historical formation of the geographic distributions of the three groups in the species, as inferred by the phylogenetic and phylogeographic analyses. (After Tominaga et al. 2016)

Further analyses of the species distributed across Japanese and continental regions will confirm the generality of those processes.

7.4 "Species" Diversity: An Estimation

Molecular phylogenetic and phylogeographic analyses have also revealed a number of cryptic deep lineages or species in the past three decades. Genetic divergences among those deep lineages as gauged by uncorrected sequence differences (p) of the mitochondrial cytochrome *b* gene, for example, are often equivalent to those for closely related species and subspecies (average uncorrected $p = 1.3\text{–}11.0\,\%$ for deep lineages of 11 selected species versus $p = 3.3\text{–}13.1\,\%$ for closest (sub)species of 10 selected species pairs) (Fig. 7.6; Appendix 3).

It is often difficult to objectively rank closely related, but genetically distinct, allopatric populations as different species, subspecies, or variations within a taxon. Such ranking or species delimitation problems are often encountered in studies of freshwater fishes. Laboratory tests for postzygotic reproductive isolation are not necessarily viable for freshwater fishes, because distinct species often produce fertile hybrids. Some regional populations can be distinguished by morphological differences, but others cannot be morphologically separated despite having similar levels of genetic differentiation. However, if the purpose of biological classification is to distinguish and name evolutionarily independent units (hereafter referred to as evolutionary units) and then construct a general reference system for biology and conservation, recognizing and naming regional groups that have been historically isolated and are expected to involve regional adaptation [i.e., category I sensu Avise (2000), ESUs, subspecies, or cryptic species] will serve that purpose.

According to Kawanabe et al. (2001), Nakabo (2013), and other recent studies, a total of 181 freshwater fish taxa (species or subspecies), restricted to those that either mostly spend their life in freshwater or to diadromous fishes that reproduce in freshwater, are recognized from the Japanese Archipelago (not including the Ryukyu Archipelago) (Appendix 4; as of September 2015). It should be mentioned that some cyprinids, a number of loaches, and a stickleback have been added to the faunal list of Japan during the last decade (see Appendix 4). Of the 181 species/subspecies, however, 31 (17.1 %) have not been given a scientific name (Fig. 7.7).

The total number of freshwater fish taxa will increase to at least 244 (a 34.8 % increase), when the deep "intraspecific" lineages that have been revealed by phylogenetic/phylogeographic analyses are added to the foregoing number as evolutionary units. In other words, only 61.5 % of the 244 forms are currently scientifically named (Fig. 7.7).

Separation and naming of different evolutionary units are crucially important not only in biological studies (e.g., selection and comparison of adequate materials), but also in conservation and management of wild and captive organisms (Moritz 1994; Frankham et al. 2002). The loss of identity of regional populations from extinction or hybridization caused by artificial introduction is equivalent to losing

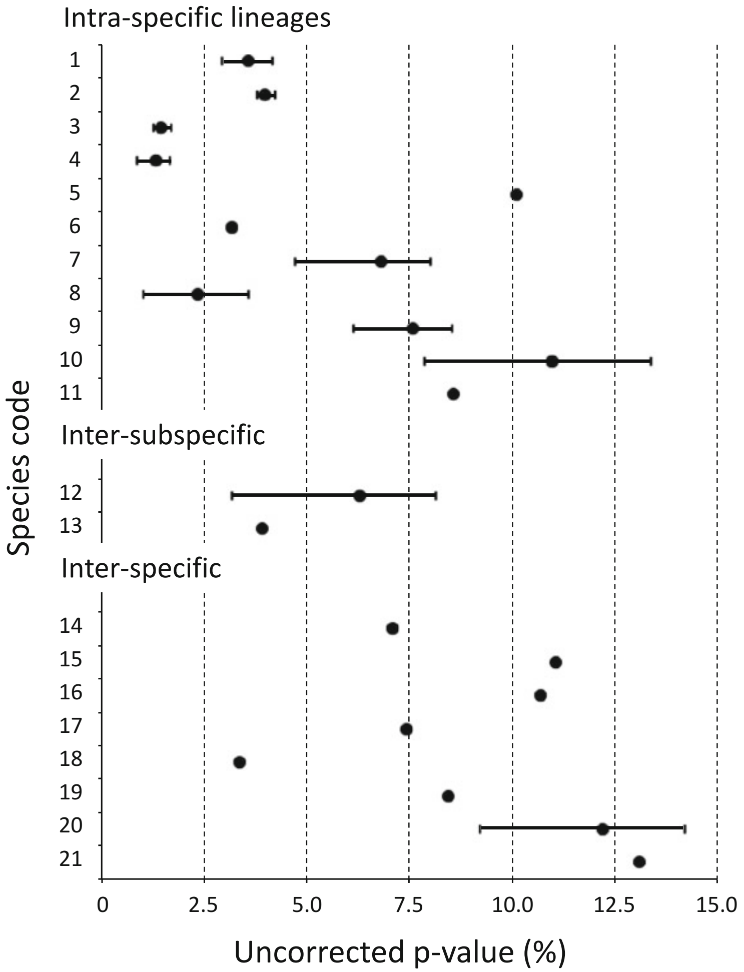


Fig. 7.6 Comparisons of the levels of genetic divergence (as uncorrected p values for the mtDNA cytochrome b gene) among intraspecific deep lineages, subspecies, and closest species pairs. A *dot* and a *horizontal line* indicate the mean and the range, respectively. Species code: *1 Tanakia lanceolata*, *2 Tanakia limbata*, *3 Acheilognathus cyanostigma*, *4 Rhodeus ocellatus kurumeus*, *5 Hemigrammocypris rasborella*, *6 Sarcocheilichthys variegatus variegatus*, *7 Gnathopogon elongatus elongatus*, *8 Biwia zezera*, *9 Pseudogobio esocius*, *10 Lefua echigonia*, *11 Liobagrus reinii*, *12 Acheilognathus tabira*, *13 Tribolodon brandtii*, *14 Acheilognathus typus–A. longipinnis*, *15 Nipponocypris temminckii–N. sieboldii*, *16 Rhynchocypris lagowskii steindachneri–R. oxycephalus jouyi*, *17 Pseudorasbora pumila–P. pugnax*, *18 Gnathopogon elongatus–G. caerulescens*, *19 Biwia zezera–B. yodoensis*, *20 Cobitis biwae* complex, *21 Lefua echigonia–Lefua* sp. Refer to Appendix 3 for the detailed data and original references

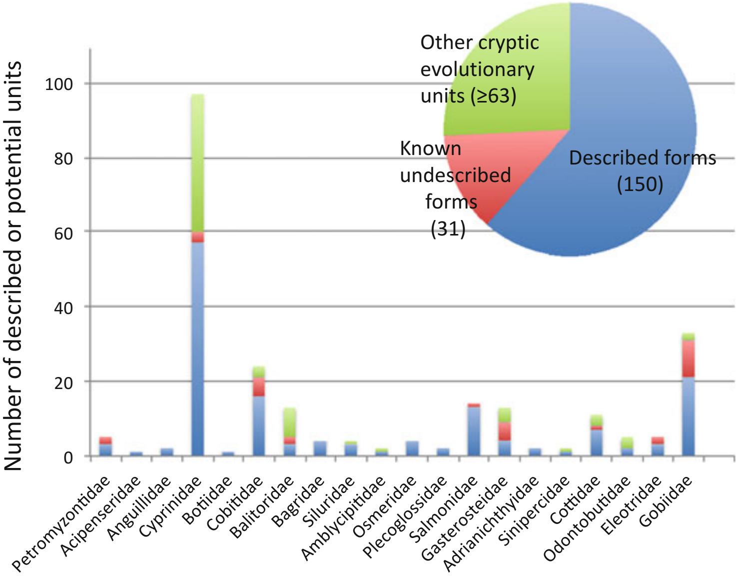


Fig. 7.7 Proportions of described (named) forms, known undescribed forms, and other cryptic evolutionary units of fishes that depend heavily on freshwater environments in the Japanese Archipelago. *Bar chart* each family, *pie chart* total. (See Appendix 4 for details)

several thousand to million years of evolutionary historical information, especially for taxonomic groups with low dispersal ability and remarkable geographic differentiation, such as freshwater fishes.

A homogenization analysis of biotas (Rahel 2000) of strictly freshwater fishes in Japan indicated that faunal similarity among the 27 regions shown in Fig. 7.2 (original, average 25.9 %) shows a 9.0 % increase across the Japanese Archipelago, primarily caused by artificial introduction (Watanabe 2012). This homogenization, or loss of β-diversity, is mostly caused by the introduction of Japanese species (8.6 % increase), especially from Lake Biwa, to other regions in Japan via intentional or unintentional introduction from fishery stocking (accounting for more than 50 % of the total introduction events; Watanabe 2012). This evaluation of homogenization, however, greatly underestimates the loss of evolutionary information associated with the disturbance of geographic distribution by human activities, because the analysis does not consider translocation of individuals between different evolutionary units within species ranges, that is, the potential mixing and replacing of different evolutionary units.

The geographic structure of indigenous species and biotas allows us to understand the dynamic geographic and environmental history of a region. A significant part of the biogeographic information of freshwater fishes has been lost via the local extirpation of species and admixture of populations by fisheries stocking, as well as pseudo-conservation actions, during the past several decades in Japan (Watanabe

2012; Nature Conservation Committee of Ichthyological Society of Japan 2013). By contrast, we have just begun scientific exploration of the complex history of the speciation and adaptive evolution of biotas with molecular techniques. Before losing further biogeographic information, we should promote studies that conduct exhaustive phylogeographic analyses over Japanese, continental and adjacent regions. Taxonomic studies that name evolutionarily distinct units are a matter of great urgency, especially for conservation purposes. Studies using new genomic approaches should also be advanced to deepen our understanding of the formation processes of biotas. In addition, greater efforts should be made to slow the tempo of the loss of historical information contained in the geographic structure of biotas to bequeath it as a legacy to future generations.

Acknowledgments We thank Kohji Mabuchi and Hiroshi Takahashi for suggestions that improved this review. This study was supported in part by JSPS KAKENHI (nos. 21370035, 26291079, and 26250044).

Appendices

Appendix 1

Data and methods for analyses of faunal patterns of Japanese freshwater fishes

Data

Regions Freshwater fish assemblages from the four main islands of the Japanese Archipelago (Kyushu, Shikoku, Honshu, and Hokkaido) were analyzed (Watanabe 2012). Regions were divided into the following 27 areas based on straits, primary watersheds (Takahashi and Sakaguchi 1976), and other watersheds that separated fish faunas (Fig. 7.2):(1) Ky-SE (southeastern Kyushu), (2) Ky-SW (southwestern Kyushu), (3) Ky-NW (northwestern Kyushu), (4) Ky-NE (northeastern Kyushu), (5W) Sh-SW (southwestern Shikoku), (5E) Sh-SE (southeastern Shikoku), (6W) Sh-NW (northwestern Shikoku), (6E) Sh-NE (northeastern Shikoku), (7) Ch-SW (southwestern Chugoku Region), (8) Ch-SE (southeastern Chugoku Region; eastern Sanyo), (9) Ch-N (northern Chugoku Region; San'in), (10) Ki-M (middle Kinki Region), (11) Ki-N (northern Kinki Region), (12) Ki-S (southern Kinki Region), (13) Tk-I (Tokai Region around Ise Bay), (14) Tk-E (eastern Tokai Region), (15) Ho-W (western Hokuriku Region), (16) Ho-E (eastern Hokuriku Region), (17) Ka (Kanto Region), (18) To-P (Pacific side of Tohoku Region), (19) To-J (Japan Sea side of Tohoku Region), (20) Hk-WS (southern southwestern Hokkaido), (21) Hk-WN (northern southwestern Hokkaido), (22) Hk- MS (southern middle Hokkaido), (23) Hk-MN (northern middle Hokkaido), (24) Hk-ES (southern eastern Hokkaido), and (25) Hk-EN (northern eastern Hokkaido).

Fishes Ninety-three forms (species, subspecies, and intraspecific monophyletic groups detected by genetic studies) of 32 genera in 8 families occurring in Japan were used in the analysis (primarily based on Nakabo 2000; Kawanabe et al. 2001). These forms included almost all primary freshwater fishes and some secondary taxa (sensu Myers 1949), excluding several species whose original distribution was uncertain, and any diadromous fishes and their sister forms (e.g., landlocked salmonids, sculpins, and gobies). Intraspecific monophyletic groups were defined as those that meet the conditions of categories I or II of Avise (2000); that is, regional allopatric populations associated with deeply separated gene (mostly mtDNA) lineages. Note that the classification (species identity, scientific names, and Japanese common names) is not updated from that used by Watanabe (2012). The presence/absence data for each fish form were obtained from papers, monographs, books, and other literature sources (see Watanabe 1998 for primary references).

Methods

The structures of the freshwater fish faunas were analyzed using parsimony analysis of endemicity (PAE) (Watanabe 2012) and a cluster analysis by unweighted pair-group method with arithmetic mean (UPGMA) based on the presence/absence matrix.

PAE The calculation for PAE using the distribution data of 93 forms and 27 areas (see following table) was conducted using PAUP*4.0b10 (Swofford 2002). The strict consensus tree was calculated from the most parsimonious area cladograms, with changes in the distribution of each fish parsimoniously reconstructed on the consensus tree under the DELTRAN criterion (Wiley et al. 1991). Endemic areas were defined as the areas or "monophyletic" clades of areas in the consensus tree that were involved with one or more "autapomorphic" or "synapomorphic" (i.e., endemic) fish forms with $\mathrm{CI} = 1.0$ (without homoplasy). The robustness of each clade was evaluated by bootstrap analysis (Felsenstein 1985) with 1000 replications.

UPGMA The presence/absence data were summarized by calculating the pairwise Jaccard's coefficient of percentage faunal similarity: $J = [a/(a+b+c)] \times 100\ \%$, where a is the number of fish forms shared between the two regions being compared, b is the number of fish forms found only in the first area, and c is the number of fish forms found only in the second area (Jaccard 1908). Based on the similarity matrix, UPGMA clustering was conducted using the NEIGHBOR program in PHYLIP 3.6 (Felsenstein 2005).

Data Source for Appendix 1

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791

Felsenstein J (2005) PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle. http://evolution.genetics.washington.edu/phylip.html. Accessed 8 Sept 2011

Jaccard P (1908) Nouvelles rescherches sur la distribution florale. Bull Soc Vaud Sci Nat 44:223–270

Kawanabe H, Mizuno N, Hosoya K (2001) Freshwater fishes of Japan, 3rd edn. Yama-Kei Publishers, Tokyo

Myers GS (1949) Salt tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijdr Dierkd 28:315–322

Nakabo T (2000) Fishes of Japan with pictorial keys to the species, 2nd edn. Tokai University Press, Tokyo

Swofford DL (2002) PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4b10. Sinauer, Sunderland

Takahashi Y, Sakaguchi Y (1976) Rivers in Japan. Kagaku 46:488–499

Watanabe K (1998) Parsimony analysis of the distribution pattern of Japanese primary freshwater fishes, and its application to the distribution of the bagrid catfishes. Ichthyol Res 45:259–270

Watanabe K (2012) Faunal structure of Japanese freshwater fishes and its artificial disturbance. Environ Biol Fish 94:533–547

Wiley EO, Siegel-Causey D, Brooks DR, Funk VA (1991) The compleat cladist: a primer of phylogenetic procedures. Museum of Natural History, University of Kansas, Lawrence

Distribution data for native strictly freshwater fishes in the Japanese Archipelago (presence = 1/absence = 0)

Taxon			Region																											
Code	Species/group	Japanese name	1	2	3	4	5W	5E	6W	6E	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	OG
Cyprinidae																														
T01	*Carassius cuvieri*	Gengoro-buna	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T02	*C. auratus grandoculis*	Nigoro-buna	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T03	*Tanakia tanago*	Miyako-tanago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
T04	*T. lanceolata*	Yari-tanago	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
T05	*T. limbata*	Aburabote	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T06	*Acheilognathus melanogaster*	Tanago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
T07	*A. tabira tabira*	Shirohire-tabira	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T08	*A. tabira erythropterus*	Akahire-tabira	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
T09	*A. tabira tohokuensis*	Kitanoakahire-tabira	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
T10	*A. tabira jordani*	Minamiakahiretabira	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
T11	*A. tabira nakamurae*	Seboshi-tabira	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T12	*A. rhombeus*	Kanehira	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T13	*A. cyanostigma*	Ichimonji-tanago	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T14	*A. longipinnis*	Itasenpara	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
T15	*A. typus*	Zeni-tanago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
T16	*Rhodeus ocellatus kurumeus*	Nipponbara-tanago	0	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T17	*R. atremius atremius*	Kazetoge-tanago	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T18	*R. atremius suigensis*	Suigenzeni-tanago	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T19	*Ischikauia steenackeri*	Wataka	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T20	*Hemigrammocypris rasborella*	Kawabata-moroko	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
T21	*Opsariichthys uncirostris*	Hasu	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued)

Distribution data for native strictly freshwater fishes in the Japanese Archipelago (presence = 1/absence = 0)

Taxon			Region																											
Code	Species/group	Japanese name	1	2	3	4	5W	5E	6W	6E	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	OG
T22	*Zacco platypus*	Oikawa	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
T23	*Z. temminckii*	Kawamutsu	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
T24	*Z. sieboldii*	Numamutsu	0	1	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
T25	*Aphyocypris chinensis*	Hina-moroko	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T26	*Rhynchocypris percnurus sachalinensis*	Yachi-ugui	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
T27	*R. lagowskii* (Japanese clade)	Aburahaya	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
T28	*R. oxycephalus* (Japanese clade)	Takahaya	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0
T29	*Pseudorasbora parva*	Motsugo	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
T30	*P. pumila pumila*	Shinai-motsugo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
T31	*P. pumila* subsp.	Ushi-motsugo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T32	*Sarcocheilichthys biwaensis*	Abura-higai	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T33	*S. variegatus variegatus*	Kawa-higai	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T34	*S. variegatus microoculus*	Biwa-higai	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T35	*Pungtungia herzi*	Mugitsuku	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T36	*Gnathopogon elongatus*	Tamoroko	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
T37	*G. caerulescens*	Honmoroko	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T38	*G. suwae*	Suwamoroko	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
T39	*Biwia zezera*	Zezera	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T40	*Biwia* sp.	Yodo-zezera	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T41	*Pseudogobio esocinus*	Kamatsuka	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0

T42	*Abbottina rivularis*	Tsuchifuki	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T43	*Hemibarbus longirostris*	Zunaganigoi	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T44	*H. labeo*	Kourai-nigoi	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T45	*H. barbus*	Nigoi	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0
T46	*Squalidus gracilis gracilis*	Ito-moroko	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T47	*S. japonica japonica*	Deme-moroko	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T48	*S. chankaensis biwae*	Sugo-moroko	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T49	*S. chankaensis* subsp.	Kourai-moroko	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cobitidae																														
T50	*Leptobotia curta*	Ayumodoki	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T51	*Misgurnus anguillicaudatus*	Dojo	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
T52	*Niwaella delicata* (Group G)	Ajime-dojo G	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T53	*Niwaella delicata* (Group S)	Ajime-dojo S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
T54	*Cobitis takatsuensis*	Ishi-dojo	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T55	*C. shikokuensis*	Hinaishi-dojo	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T56	*C. biwae* (Eastern)	Shima-dojo E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
T57	*C. biwae* (Kochi)	Shima-dojo K	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T58	*C. biwae* (Western)	Shima-dojo W	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
T59	*C.* sp. Y86	Yamatoshima-dojo Y86	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T60	*C.* sp. Y90	Yamatoshima-dojo Y90	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T61	*C.* sp. Y94	Yamatoshima-dojo Y94	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T62	*C.* sp. 3 (Middle)	Sujishima-dojo M	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued)

Distribution data for native strictly freshwater fishes in the Japanese Archipelago (presence = 1/absence = 0)

Taxon			Region																											
Code	Species/group	Japanese name	1	2	3	4	5W	5E	6W	6E	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	OG
T63	*C*. sp. 2 subsp. 1 (Small-Sanyo)	Sujisima-dojo S-SY	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T64	*C*. sp. 2 subsp. 2 (Small-Tokai)	Sujisima-dojo S-T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
T65	*C*. sp. 2 subsp. 3 (Small-San'in)	Sujisima-dojo S-SI	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T66	*C*. sp. 2 subsp. 4 (Small-Kyushu)	Sujisima-dojo S-K	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T67	*C*. sp. 2 subsp. 5 (Small-L.Biwa)	Sujisima-dojo S-B	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T68	*C*. sp. 2 subsp. 6 (Small-R.Yodo)	Sujisima-dojo S-Y	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T69	*C*. sp. 1 (Large)	Sujisima-dojo L	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T70	*Noemacheilus barbatulus toni*	Fuku-dojo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
T71	*Lefua nikkonis*	Ezohotoke-dojo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
T72	*L. echigonia* (Hokuriku)	Hotoke-dojo Hokuriku	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
T73	*L. echigonia* (Tohoku)	Hotoke-dojo Tohoku	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
T74	*L. echigonia* (Tokai)	Hotoke-dojo Tokai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
T75	*L. echigonia* (Kinki)	Hotoke-dojo Kinki	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
T76	*L. echigonia* (N-Kanto)	Hotoke-dojo N-Kanto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
T77	*L. echigonia* (S-Kanto)	Hotoke-dojo S-Kanto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
T78	*L*. sp. (Kinki-Shikoku)	Nagarehotoke-dojo KS	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T79	*L*. sp. (Sanyo)	Nagarehotoke-dojo SY	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

T80	*L.* sp. (Tokai)	Nagarehotoke-dojo TK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Bagridae																														
T81	*Pseudobagrus nudiceps*	Gigi	0	0	0	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T82	*P. tokiensis*	Gibachi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
T83	*P. ichikawai*	Neko-gigi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
T84	*P. aurantiacus*	Ariake-gibachi	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siluridae																														
T85	*Silurus lithophilus*	Iwatoko-namazu	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T86	*S. biwaensis*	Biwakooo-namazu	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T87	*S. asotus*	Namazu	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Amblycipitidae																														
T88	*Liobagrus reini*	Akaza	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Adrianichthyidae																														
T89	*Oryzias latipes* subsp.	Medaka N	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
T90	*O. latipes latipes*	Medaka S	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0
Sinipercidae																														
T91	*Coreoperca kawamebari*	Oyanirami	0	1	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontobutiidae																														
T92	*Odontobutis obscura*	Donko	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
T93	*O. hikimius*	Ishi-Donko	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

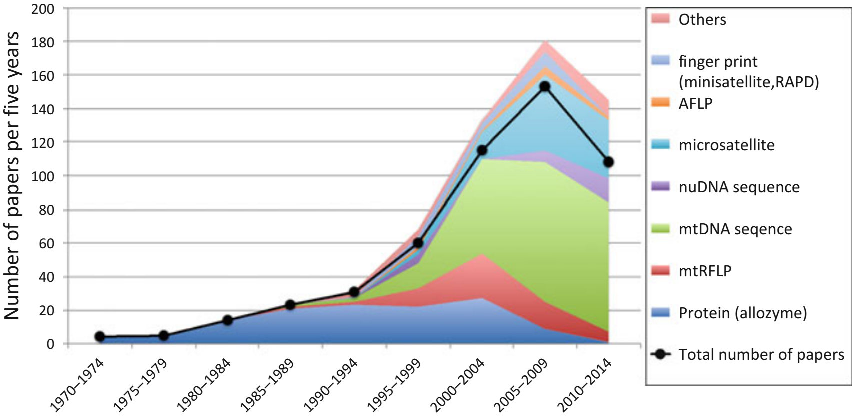
For region codes, see text and Fig. 7.2

The data shown are as used by Watanabe (2012); scientific names and Japanese common names have not been updated

Appendix 2

Total number of papers per 5 years using each type of molecular marker.

Data from the database GEDIMAP (http://gedimap.zool.kyoto-u.ac.jp), retrieved on 20 August 2015



Appendix 3

Comparisons of the levels of genetic divergence (as uncorrected *p* values for the mtDNA cytochrome *b* gene) among intraspecific deep lineages, subspecies, and closest species pairs

Code	Species	Details	Original source	Sequence region	Minimum	Maximum	Mean	Remark
Intraspecific								
1	*Tanakia lanceolata*	4 lineages (LA1, LA2, LA3, LA4)	Hashiguchi et al. (2006)	Full	0.0292	0.0416	0.0357	1
2	*Tanakia limbata*	3 (LI1, LI2, LI3)	Hashiguchi et al. (2006)	Full	0.0378	0.0424	0.0397	1
3	*Acheilognathus cyanostigma*	3 (Clades 1, 2, 3)	Kitazima et al. (2015)	Full	0.0126	0.0171	0.0147	1
4	*Rhodeus ocellatus kurumeus*	3 (Osaka, Okayama, Kyushu)	Abe et al. (2013)	Full	0.0088	0.0167	0.0134	1
5	*Hemigrammocypris rasborella*	2 (Honshu+Shikoku, Kyushu)	Watanabe et al. (2014)	Full			0.1011	2
6	*Sarcocheilichthys variegatus variegatus*	2 (A+B+C+D, E)	Komiya et al. (2014)	3′-half			0.0317	1
7	*Gnathopogon elongatus elongatus*	3 (E1, E2, E3)	Kakioka et al. (2013)	Full	0.0471	0.0800	0.0682	1
8	*Biwia zezera*	4 (ISE, LBW, SNY, KYS)	Watanabe et al. (2010a, b)	Full	0.0102	0.0357	0.0236	1
9	*Pseudogobio esocius*	3 (Groups A, B, C)	Tominaga et al. (2016)	Full	0.0615	0.0855	0.0757	1
10	*Lefua echigonia*	5 of 8 (Tohoku, Echigo, North-Kanto, South-Kanto, Tokai–Kinki)	Saka et al. (2003)	Full	0.0785	0.1336	0.1098	1
11	*Liobagrus reinii*	2 (Groups 1, 2)	Nakagawa et al. (2016)	Full			0.0856	2
						n	11	
						Average	0.0545	
						SD	0.0349	
						Minimum	0.0134	
						Maximum	0.1098	
Inter-subspecific								
12	*Acheilognathus tabira*	5 subspp.	Kitamura et al. (2012)	Full	0.0317	0.0814	0.0630	1
13	*Tribolodon brandtii*	2 subspp.	Watanabe and Sakai et al. (unpublished data)	3′-half			0.0391	1

(continued)

Code	Species	Details	Original source	Sequence region	Minimum	Maximum	Mean	Remark
Interspecific								
14	*Acheilognathus typus–A. longipinnis*		Kawamura et al. (2014)	Full			0.0710	1
15	*Nipponocypris temminckii–N. sieboldii*		Saitoh et al. (2006) and Miya et al. (2015)	Full			0.1105	1
16	*Rhynchocypris lagowskii steindachneri–R. oxycephalus jouyi*		Sasaki et al. (2008)	Full			0.1070	1
17	*Pseudorasbora pumila–P. pugnax*		Kakioka et al. (2013)	Full			0.0742	1
18	*Gnathopogon elongatus–G. caerulescens*		Kakioka et al. (2013)	Full			0.0335	2
19	*Biwia zezera–B. yodoensis*		Watanabe et al. (2010)	Full			0.0845	1
20	*Cobitis* spp. BIWAE complex		Kitagawa et al. (2003)	5′-half	0.0920	0.1420	0.1220	1
21	*Lefua echigonia–L.* sp.		Saka et al. (2003)	Full			0.1309	1
						n	10	
						Average	0.0836	
						SD	0.0336	
						Minimum	0.0335	
						Maximum	0.1309	

Remark: *1* recalculated, *2* described in the original reference

Data Source for Appendix 3

Abe T, Kobayashi I, Watanabe K (2013) An extant native population of the Japanese rosy bitterling, *Rhodeus ocellatus kurumeus*, in the Sanyo Region, western Japan. Jpn J Ichthyol 60:49–55

Hashiguchi Y, Kado T, Kimura S, Tachida H (2006) Comparative phylogeography of two bitterlings, *Tanakia lanceolata* and *T. limbata* (Teleostei, Cyprinidae), in Kyushu and adjacent districts of western Japan, based on mitochondrial DNA analysis. Zool Sci 23:309–322

Kakioka R, Kokita T, Tabata R, Mori S, Watanabe K (2013) The origins of limnetic forms and cryptic divergence in *Gnathopogon* fishes (Cyprinidae) in Japan. Environ Biol Fish 96:631–644

Kawamura K, Ueda T, Arai R, Smith C (2014) Phylogenetic relationships of bitterling fishes (Teleostei: Cypriniformes: Acheilognathinae), inferred from mitochondrial cytochrome *b* sequences. Zool Sci 31:321–329

Kitagawa T, Watanabe M, Kitagawa E, Yoshioka M, Kashiwagi M, Okazaki T (2003) Phylogeography and the maternal origin of the tetraploid form of the Japanese spined loach, *Cobitis biwae*, revealed by mitochondrial DNA analysis. Ichthyol Res 50:318–325

Kitamura J, Nagata N, Nakajima J, Sota T (2012) Divergence of ovipositor length and egg shape in a brood parasitic bitterling fish through the use of different mussel hosts. J Evol Biol 25:566–573

Kitazima J, Matsuda M, Mori S, Kokita T, Watanabe K (2015) Population structure and cryptic replacement of local populations in the endangered bitterling *Acheilognathus cyanostigma*. Ichthyol Res 62:122–130

Komiya T, Fujita-Yanahibayashi S, Watanabe K (2014) Multiple colonizations of Lake Biwa by *Sarcocheilichthys* fishes and their population history. Environ Biol Fish 97:741–755

Miya M, Sato Y, Fukunaga T, Sado T, Poulsen JY, Sato K, Minamoto T, Yamamoto S, Yamanaka H, Araki H, Kondoh M, Iwasaki W (2015) MiFish, a set of universal PCR primers for metabarcoding environmental DNA from fishes: detection of more than 230 subtropical marine species. R Soc Open Sci 2:150088. doi:10.1098/rsos.150088

Nakagawa H, Seki S, Ishikawa T, Watanabe K (2016) Genetic population structure of the Japanese torrent catfish *Liobagrus reinii* (Amblycipitidae), inferred from mitochondrial cytochrome *b* variations. Ichthyol Res 63:333–346

Saitoh K, Sado T, Mayden RL, Hanzawa N, Nakamura K, Nishida M, Miya M (2006) Mitogenomic evolution and interrelationships of the Cypriniformes (Actinopterygii: Ostariophysi): the first evidence toward resolution of higher-level relationships of the world's largest freshwater fish clade based on 59 whole mitogenome sequences. J Mol Evol 63:826–841

Saka R, Takehana Y, Suguro N, Sakaizumi M (2003) Genetic population structure of *Lefua echigonia* inferred from allozymic and mitochondrial cytochrome *b* variations. Ichthyol Res 50:140–148

Sasaki T, Kartavtsev YP, Chiba SN, Uematsu T, Sviridov VV, Hanzawa N (2007) Genetic divergence and phylogenetic independence of Far Eastern species in subfamily Leuciscinae (Pisces: Cyprinidae) inferred from mitochondrial DNA analyses. Genes Genet Syst 82:329–340

Tominaga K, Nakajima J, Watanabe K (2016) Cryptic divergence and phylogeography of the pike gudgeon *Pseudogobio esocinus* (Teleostei: Cyprinidae): a comprehensive case of freshwater phylogeography in Japan. Ichthyol Res 63:79–93

Watanabe K, Kawase S, Mukai T, Kakioka R, Miyazaki J-I, Hosoya K (2010) Population divergence of *Biwia zezera* (Cyprinidae: Gobioninae) and the discovery of a cryptic species, based on mitochondrial and nuclear DNA sequence analyses. Zool Sci 27:647–655

Watanabe K, Mori S, Tanaka T, Kanagawa N, Itai T, Kitamura J, Suzuki N, Tominaga K, Kakioka R, Tabata R, Abe T, Tashiro Y, Hashimoto Y, Nakajima J, Onikura N (2014) Genetic population structure of *Hemigrammocypris rasborella* (Cyprinidae) inferred from mtDNA sequences. Ichthyol Res 61:352–360

Appendix 4

A list of species, subspecies, and distinct intraspecific deep lineages of freshwater fishes occurring in the Japanese Archipelago (not including the Ryukyu Islands).

Only species that largely spend their lives in freshwater or diadromous fishes that reproduce in freshwater are included. This list is NOT an effective publication under the International Code of Zoological Nomenclature.

ID	Family	Scientific name	Japanese common name	Unpublished	Undescribed/ undetermined	Increment	Un-named	Nakabo (2013)	Kawanabe et al. (2001)	Described after, or not included in Nakabo (2013)	Described in and after 2000	Tentative name	Reference(s) relating to cryptic lineages
1	Petromyzontidae	*Entosphenus tridentatus*	Mitsuba-yatsume					*Entosphenus tridentatus*	*Entosphenus tridentatus*				
2	Petromyzontidae	*Lethenteron* sp. N	Suna-yatsume “Hoppou-shu”		1		1	*Lethenteron* sp. N	*Lethenteron reissneri*				Yamazaki and Goto (1996, 1998) and Yamazaki et al. (2003, 2006)
3	Petromyzontidae	*Lethenteron* sp. S	Suna-yatsume “Nanpou-shu”		1		1	*Lethenteron* sp. S	*Lethenteron reissneri*				Yamazaki and Goto (1996, 1998) and Yamazaki et al. (2003, 2006)
4	Petromyzontidae	*Lethenteron kessleri*	Siberia-yatsume					*Lethenteron kessleri*	*Lethenteron kessleri*				
5	Petromyzontidae	*Lethenteron japonicum*	Kawa-yatsume					*Lethenteron japonicum*	*Lethenteron japonicum*				
6	Acipenseridae	*Acipenser medirostris*	Chozame					*Acipenser medirostris*	*Acipenser medirostris*				
7	Anguillidae	*Anguilla japonica*	Nihon-unagi					*Anguilla japonica*	*Anguilla japonica*				
8	Anguillidae	*Anguilla marmorata*	Oo-unagi					*Anguilla marmorata*	*Anguilla marmorata*				
9	Cyprinidae	*Cyprinus melanotus?*	Koi		1			*Cyprinus carpio*	*Cyprinus carpio*			Nogoi	Mabuchi et al. (2005, 2008)
10	Cyprinidae	*Carassius cuvieri*	Gengorobuna					*Carassius cuvieri*	*Carassius cuvieri*				
11	Cyprinidae	*Carassius* sp.	Ginbuna		1		1	*Carassius* sp.	*Carassius* sp.				Shimizu Y et al. (1993) and Takada et al. (2010)
12	Cyprinidae	*Carassius buergeri grandoculis*	Nigorobuna					*Carassius buergeri grandoculis*	*Carassius buergeri grandoculis*				
13	Cyprinidae	*Carassius buergeri* subsp. 1	Nagabuna		1		1	*Carassius buergeri* subsp. 1	*Carassius buergeri* subsp. 2				Shimizu Y et al. (1993) and Takada et al. (2010)
14	Cyprinidae	*Carassius buergeri* subsp. 2	Kinbuna		1		1	*Carassius buergeri* subsp. 2	*Carassius buergeri* subsp. 1				Shimizu Y et al. (1993) and Takada et al. (2010)
15	Cyprinidae	*Carassius buergeri buergeri*	Oo-kinbuna					*Carassius buergeri buergeri*	*Carassius buergeri buergeri*				
16	Cyprinidae	*Tanakia tanago*	Miyako-tanago					*Tanakia tanago*	*Tanakia tanago*				
17	Cyprinidae	*Tanakia lanceolata*	Yari-tanago		≥4	3		*Tanakia lanceolata*	*Tanakia lanceolata*			At least 4 regional groups have been known (LA1–4), but no exhaustive analysis has been published	Hashiguchi et al. (2006) and Matsuba et al. (2014)
18	Cyprinidae	*Tanakia limbata*	Aburabote		≥3	2		*Tanakia limbata*	*Tanakia limbata*			At least 3 regional groups have been known (LI1–3), but no exhaustive analysis has been published	Hashiguchi et al. (2006) and Matsuba et al. (2014)

(continued)

ID	Family	Scientific name	Japanese common name	Unpublished	Undescribed/ undetermined	Increment	Un-named	Nakabo (2013)	Kawanabe et al. (2001)	Described after, or not included in Nakabo (2013)	Described in and after 2000	Tentative name	Reference(s) relating to cryptic lineages
19	Cyprinidae	*Acheilognathus rhombeus*	Kanehira					*Acheilognathus rhombeus*	*Acheilognathus rhombeus*				
20	Cyprinidae	*Acheilognathus cyanostigma*	Ichimonji-tanago		3	2		*Acheilognathus cyanostigma*	*Acheilognathus cyanostigma*			Ichimonji-tanago "clade 1", "clade 2", "clade 3"	Kitazima et al. (2015)
21	Cyprinidae	*Acheilognathus melanogaster*	Tanago					*Acheilognathus melanogaster*	*Acheilognathus melanogaster*				
22	Cyprinidae	*Acheilognathus longipinnis*	Itasenpara		3	2		*Acheilognathus longipinnis*	*Acheilognathus longipinnis*			Itasenpara "Lake Biwa–Yodo", "Nobi", "Toyama"	Okazaki et al. (2006) and Kitanishi et al. (2013)
23	Cyprinidae	*Acheilognathus tabira jordani*	Minamiakahire-tabira					*Acheilognathus tabira jordani*	*Acheilognathus tabira* subsp. R		1		Kitamura et al. (2012)
24	Cyprinidae	*Acheilognathus tabira nakamurae*	Seboshi-tabira					*Acheilognathus tabira* nakamurae	*Acheilognathus tabira* subsp. S		1		Kitamura et al. (2012)
25	Cyprinidae	*Acheilognathus tabira tabira*	Shirohire-tabira					*Acheilognathus tabira tabira*	*Acheilognathus tabira tabira*				Kitamura et al. (2012)
26	Cyprinidae	*Acheilognathus tabira erythropterus*	Akahire-tabira					*Acheilognathus tabira erythropterus*	*Acheilognathus tabira* subsp. R		1		Kitamura et al. (2012)
27	Cyprinidae	*Acheilognathus tabira tohokuensis*	Kitanoakahire-tabira					*Acheilognathus tabira tohokuensis*	*Acheilognathus tabira* subsp. R		1		Kitamura et al. (2012)
28	Cyprinidae	*Acheilognathus typus*	Zeni-tanago					*Acheilognathus typus*	*Acheilognathus typus*				
29	Cyprinidae	*Rhodeus ocellatus kurumeus*	Nipponbara-tanago		≥3	2		*Rhodeus ocellatus kurumeus*	*Rhodeus ocellatus kurumeus*			At least 3 regional groups have been known (Osaka, Sanyo, Kyushu), but no exhaustive analysis has been published	Abe et al. (2013)
30	Cyprinidae	*Rhodeus smithii atremius*	Kazetoge-tanago					*Rhodeus smithii smithii*	*Rhodeus atremius atremius*				Miyake et al. (2011)
31	Cyprinidae	*Rhodeus smithii smithii*?	Suigenzeni-tanago		1			*Rhodeus smithii smithii*	*Rhodeus atremius suigensis*				Miyake et al. (2011)
32	Cyprinidae	*Ischikauia steenackeri*	Wataka					*Ischikauia steenackeri*	*Ischikauia steenackeri*				
33	Cyprinidae	*Hemigrammocypris rasborella* (*H. neglectus*?)	Kawabatamoroko		≥2	1		*Hemigrammocypris rasborella*	*Hemigrammocypris rasborella*	*Hemigrammocypris neglectus* (Stieler 1907): Zarske (2013)		Kawabatamoroko "Honshu–Shikoku", "Kyushu"; A total of 4 regional population groups are included in the "Honshu–Shikoku" group	Watanabe et al. (2014)
34	Cyprinidae	*Opsariichthys uncirostris uncirostris*	Hasu					*Opsariichthys uncirostris uncirostris*	*Opsariichthys uncirostris uncirostris*				

35	Cyprinidae	*Zacco platypus*	Oikawa	1	≥3	2		*Opsariichthys platypus*	*Zacco platypus*			At least 3 regional groups have been known, but not yet published	Kitanishi et al. (2016)
36	Cyprinidae	*Nipponocypris temminckii*	Kawamutsu	1	≥3	2		*Candidia temminckii*	*Zacco temmincki*			At least 3 regional groups have been known, but not yet published	Matsuoka et al. (unpublished data) and Watanabe et al. (unpublished data)
37	Cyprinidae	*Nipponocypris sieboldii*	Numamutsu	1	≥3	2		*Candidia sieboldi*				At least 3 regional groups have been known, but not yet published	Matsuoka et al. (unpublished data); Watanabe et al. (unpublished data)
38	Cyprinidae	*Aphyocypris chinensis*	Hinamoroko					*Aphyoctpris chinensis*	*Aphyoctpris chinensis*				
39	Cyprinidae	*Rhynchocypris percnurus sachalinensis*	Yachiugui					*Phoxinus percnurus sachalinensis*	*Phoxinus percnurus sachalinensis*				
40	Cyprinidae	*Rhynchocypris lagowskii steindachneri*	Aburahaya					*Phoxinus lagowskii steindachneri*	*Phoxinus lagowskii steindachneri*				
41		*Rhynchocypris lagowskii yamamotis*	Yamanakahaya					*Phoxinus lagowskii yamamotis*					
42	Cyprinidae	*Rhynchocypris oxycephalus jouyi*	Takahaya	1	≥2	2		*Phoxinus oxycephalus jouyi*	*Phoxinus oxycephalus jouyi*			Several regional groups, but no exhaustive analysis has been published yet	Watanabe et al. (unpublished data)
43	Cyprinidae	*Tribolodon brandtii maruta*	Maruta					*Tribolodon brandtii*	*Tribolodon brandti*	*Tribolodon brandtii maruta* Sakai and Amano (2014)	1		Sakai et al. (2002) and Sasaki et al. (2007)
44	Cyprinidae	*Tribolodon brandtii brandtii*	Jusan-ugui					*Tribolodon brandtii*	*Tribolodon brandti*	*Tribolodon brandtii brandtii*			
45	Cyprinidae	*Tribolodon nakamurai*	Ukekuchi-ugui					*Tribolodon nakamurai*	*Tribolodon nakamurai*		1		Sakai et al. (2002) and Sasaki et al. (2007)
46	Cyprinidae	*Tribolodon sachalinensis*	Ezo-ugui					*Tribolodon sachalinensis*	*Tribolodon ezoe*				
47	Cyprinidae	*Tribolodon hakonensis*	Ugui	1	3	2		*Tribolodon hakonensis*	*Tribolodon hakonensis*			At least 3 regional groups have been known, but not yet published	Watanabe and Sakai et al. (unpublished data)
48	Cyprinidae	*Pseudorasbora parva*	Motsugo	1	4	3		*Pseudorasbora parva*	*Pseudorasbora parva*			At least 4 regional groups have been known, but not yet published	Mukai et al. (unpublished data)
49	Cyprinidae	*Pseudorasbora pumila*	Shinai-motsugo					*Pseudorasbora pumila pumila*	*Pseudorasbora pumila pumila*	*Pseudorasbora pumila*			
50	Cyprinidae	*Pseudorasbora pugnax*	Ushi-motsugo					*Pseudorasbora pumila* subsp.	*Pseudorasbora pumila* subsp.	*Pseudorasbora pugnax* Kawase and Hosoya (2015)	1		Watanabe et al. (2000) and Watanabe and Mori (2008)

(continued)

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51	Cyprinidae	*Sarcocheilichthys biwaensis*	Abura-higai					*Sarcocheilichthys biwaensis*	*Sarcocheilichthys biwaensis*				
52	Cyprinidae	*Sarcocheilichthys variegatus variegatus*	Kawa-higai		2	1		*Sarcocheilichthys variegatus variegatus*	*Sarcocheilichthys variegatus variegatus*			Kawa-higai "Tokai", "West"	Komiya et al. (2014)
53	Cyprinidae	*Sarcocheilichthys variegatus microoculus*	Biwa-higai					*Sarcocheilichthys variegatus microoculus*	*Sarcocheilichthys variegatus microoculus*				
54	Cyprinidae	*Pungtungia herzi*	Mugitsuku					*Pungtungia herzi*	*Pungtungia herzi*				
55	Cyprinidae	*Gnathopogon elongatus elongatus*	Tamoroko		3	2		*Gnathopogon elongatus elongatus*	*Gnathopogon elongatus elongatus*			Tamoroko "E1, West", "E2, Tokai", "E3, Ina"	Kakioka et al. (2013)
56	Cyprinidae	*Gnathopogon elongatus suwae*	Suwamoroko					*Gnathopogon elongatus suwae*	*Gnathopogon elongatus suwae*				
57	Cyprinidae	*Gnathopogon caerulescens*	Honmoroko					*Gnathopogon caerulescens*	*Gnathopogon caerulescens*				
58	Cyprinidae	*Biwia zezera*	Zezera		4	3		*Biwia zezera*	*Biwia zezera*			Zezera "Gifu", "Lake Biwa", "Sanyo", "Kyushu"	Watanabe et al. (2010)
59	Cyprinidae	*Biwia yodoensis*	Yodo-zezera					*Biwia yodoensis*	*Biwia zezera*		1		Watanabe et al. (2010)
60	Cyprinidae	*Pseudogobio esocinus*	Kamatsuka		≥3	2		*Pseudogobio esocinus esocinus*	*Pseudogobio esocinus esocinus*			Kamatsuka "Group A", "Group B", "Group C"; a total of 12 regional population groups are included	Tominaga et al. (2016)
61	Cyprinidae	*Abbottina rivularis*	Tsuchifuki	1	2	1		*Abbottina rivularis*	*Abbottina rivularis*			Tsuchifuki "Continental", "Japan endemic"	Jang-Liaw and Watanabe et al. (unpublished data)
62	Cyprinidae	*Hemibarbus longirostris*	Zunaga-nigoi					*Hemibarbus longirostris*	*Hemibarbus longirostris*				
63	Cyprinidae	*Hemibarbus labeo*	Korai-nigoi					*Hemibarbus labeo*					
64	Cyprinidae	*Hemibarbus barbus*	Nigoi					*Hemibarbus barbus*	*Hemibarbus barbus*				
65	Cyprinidae	*Squalidus gracilis gracilis*	Itomoroko	1	3	2		*Squalidus gracilis gracilis*	*Squalidus gracilis gracilis*			At least 8 groups of 3 major regonal groups	Watanabe et al. (unpublished data)
66	Cyprinidae	*Squalidus japonicus japonicus*	Dememoroko	1	2	1		*Squalidus japonicus japonicus*	*Squalidus japonicus japonicus*			Dememoroko "Lake Biwa", "Nobi"	Kakioka and Watanabe et al. (unpublished data)
67	Cyprinidae	*Squalidus biwae biwae*	Sugomoroko					*Squalidus chankaensis biwae*	*Squalidus chankaensis biwae*				
68	Cyprinidae	*Squalidus biwae tsuchigae*	Koraimoroko					*Squalidus chankaensis tsuchigae*	*Squalidus chankaensis* subsp.				

69	Botiidae	*Parabotia curtus*	Ayumodoki					*Parabotia curta*	*Leptobotia curta*	*Parabotia curtus*: Kottelat (2012)			
70	Cobitidae	*Misgurnus anguillicaudatus*?	Dojo		2	1		*Misgurnus anguillicaudatus*	*Misgurnus anguillicaudatus*			Group A, B-2; B-1 (introduced), other two groups are known in the Ryukyu Is. (IR, OK)	Morishima et al. (2008), Koizumi et al. (2009), Shimizu et al. (2011), Kano et al. (2011), Kitagawa et al. (2011) and Perdices et al. (2012)
71	Cobitidae	*Niwaella delicata*	Ajime-dojo		2	1		*Niwaella delicata*	*Niwaella delicata*			Ajime-dojo "G, Pacific", "S, Japan Sea"	Kitagawa et al. (2001a)
72	Cobitidae	*Cobitis takatsuensis*	Ishidojo					*Cobitis takatsuensis*	*Cobitis takatsuensis*				Kitagawa et al. (2001b) and Shimizu et al. (2004)
73	Cobitidae	*Cobitis shikokuensis*	Hina-ishidojo					*Cobitis shikokuensis*	*Cobitis takatsuensis*		1		Kitagawa et al. (2001b) and Shimizu et al. (2004)
74	Cobitidae	*Cobitis* sp. BIWAE type A	Oo-shimadojo		1		1	*Cobitis biwae*	*Cobitis biwae*	*Cobitis* sp. BIWAE type A: Nakajima et al. (2012)			Kitagawa et al. (2003)
75	Cobitidae	*Cobitis* sp. BIWAE type B	Nishi-shimadojo		1		1	*Cobitis biwae*	*Cobitis biwae*	*Cobitis* sp. BIWAE type B: Nakajima et al. (2012)			Kitagawa et al. (2003)
76	Cobitidae	*Cobitis* sp. BIWAE type C	Higashi-shimadojo		1		1	*Cobitis biwae*	*Cobitis biwae*	*Cobitis* sp. BIWAE type C: Nakajima et al. (2012)			Kitagawa et al. (2003)
77	Cobitidae	*Cobitis* sp. BIWAE type D	Tosa-shimadojo		1		1	*Cobitis biwae*	*Cobitis biwae*	*Cobitis* sp. BIWAE type D: Nakajima et al. (2012)			Kitagawa et al. (2003)
78	Cobitidae	*Cobitis matsubarae*	Yamato-shimadojo		≥2	1		*Cobitis matsubarae*	*Cobitis* sp. Y86, Y90, Y94			Yamato-shimadojo A, B (Y86, Y90, Y94)	Saitoh et al. (2000) and Kitagawa et al. (2003)
79	Cobitidae	*Cobitis* sp. 5	Tango-sujishimadojo		1		1	*Cobitis* sp.	–	See footnote (a)			Takeno et al. (2010)
80	Cobitidae	*Cobitis minamorii oumiensis*	Biwa-kogata-sujishimadojo					*Cobitis minamorii oumiensis*	*Cobitis* sp. S		1		Kitagawa et al. (2005) and Saitoh et al. (2010)
81	Cobitidae	*Cobitis magnostriata*	Oogata-sujishimadojo					*Cobitis magnostriata*	*Cobitis* sp. L		1		Kitagawa et al. (2005) and Saitoh et al. (2010)
82	Cobitidae	*Cobitis striata striata*	Chugata-sujishimadojo					*Cobitis striata striata*	*Cobitis* sp. M		1		Kitagawa et al. (2005) and Saitoh et al. (2010)
83	Cobitidae	*Cobitis minamorii minamorii*	Sanyo-kogata-sujishimadojo					*Cobitis minamorii minamorii*	*Cobitis* sp. S		1		Kitagawa et al. (2005) and Saitoh et al. (2010)
84	Cobitidae	*Cobitis minamorii tokaiensis*	Tokai-kogata-sujishimadojo					*Cobitis minamorii tokaiensis*	*Cobitis* sp. S		1		Kitagawa et al. (2005) and Saitoh et al. (2010)
85	Cobitidae	*Cobitis minamorii saninensis*	Sanin-kogata-sujishimadojo					*Cobitis minamorii saninensis*	*Cobitis* sp. S		1		Kitagawa et al. (2005) and Saitoh et al. (2010)
86	Cobitidae	*Cobitis minamorii yodoensis*	Yodo-kogata-sujishimadojo					–	*Cobitis* sp. S	*Cobitis minamorii yodoensis* Nakajima (2012)	1		Saitoh et al. (2010)

(continued)

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87	Cobitidae	*Cobitis striata fuchigamii*	Onga-sujishimadojo					–	–	*Cobitis striata fuchigamii* Nakajima (2012)	1		Kitagawa et al. (2009)
88	Cobitidae	*Cobitis striata hakataensis*	Hakata-sujishimadojo					–	–	*Cobitis striata hakataensis* Nakajima (2012)	1		Kitagawa et al. (2009)
89	Cobitidae	*Cobitis kaibarai*	Ariake-sujishimadojo					–	*Cobitis* sp. S	*Cobitis kaibarai* Nakajima (2012)	1		Kitagawa et al. (2005) and Saitoh et al. (2010)
90	Cobitidae	*Cobitis sakahoko*	Ooyodo-shimadojo					–	–	*Cobitis sakahoko* Nakajima and Suzawa (2015)	1		Nakajima et al. (2011)
91	Balitoridae	*Barbatula oreas*	Fukudojo					*Noemacheilus barbatulus toni*	*Noemacheilus barbatulus toni*	*Barbatula oreas*: Kottelat (2012)			
92	Balitoridae	*Lefua nikkonis*	Ezo-hotokedojo					*Lefua costata nikkonis*	*Lefua nikkonis*				
93	Balitoridae	*Lefua echigonia*	Hotokedojo		8	7		*Lefua echigonia*	*Lefua echigonia*			Hotokedojo “Hokuriku”, “Kinki”, “Tokai”, “Yamagata”, “Tohoku”, “North-Kanto”, “South-Kanoto”, “Iwate”	Saka et al. (2003), Sakai et al. (2003), Mihara (2005), Miyazaki et al. (2007, 2011), Aiki et al. (2009) and Takeuchi et al. (2015)
94	Balitoridae	*Lefua* sp. 1	Nagare-hotokedojo		2	1	1	*Lefua* sp. 1	*Lefua* sp.			Nagare-hotokedojo “Kii–Shikoku”, “Sanyo–Sanin”	Mihara (2005), Miyazaki et al. (2007, 2011) and Kobayashi (2008)
95	Balitoridae	*Lefua* sp. 2	Tokai-nagare-hotokedojo		1		1	*Lefua* sp. 2	*Lefua* sp.				Miyazaki et al. (2007, 2011)
96	Bagridae	*Pseudobagrus nudiceps*	Gigi					*Tachysurus nudiceps*	*Pseudobagrus nudiceps*				
97	Bagridae	*Pseudobagrus tokiensis*	Gibachi					*Tachysurus tokiensis*	*Pseudobagrus tokiensis*				
98	Bagridae	*Pseudobagrus aurantiacus*	Ariake-gibachi					*Tachysurus aurantiacus*	*Pseudobagrus aurantiacus*				
99	Bagridae	*Pseudobagrus ichikawai*	Nekogigi					*Tachysurus ichikawai*	*Pseudobagrus ichikawai*				
100	Siluridae	*Silurus lithophilus*	Iwatoko-namazu	1	2	1		*Silurus lithophilus*	*Silurus lithophilus*			Iwatoko-namazu “Lake Biwa”, “East”	Matsuzaki et al. (unpublished data) and Tabata et al. (2016)
101	Siluridae	*Silurus biwaensis*	Biwakooo-namazu					*Silurus biwaensis*	*Silurus biwaensis*				
102	Siluridae	*Silurus asotus*	Namazu					*Silurus asotus*	*Silurus asotus*				

103	Amblycipitidae	*Liobagrus reinii*	Akaza		2	1		*Liobagrus reinii*	*Liobagrus reini*			Akaza “Group 1”, “Group 2”; a total of 7 regional population groups are included	Nakagawa et al. (2016)
104	Osmeridae	*Spirinchus lanceolatus*	Shishamo					*Spirinchus lanceolatus*	*Spirinchus lanceolatus*				
105	Osmeridae	*Osmerus dentex*	Kyuriuo					*Osmerus dentex*	*Osmerus eperlanus mordax*				
106	Osmeridae	*Hypomesus nipponensis*	Wakasagi					*Hypomesus nipponensis*	*Hypomesus nipponensis*				
107	Osmeridae	*Hypomesus olidus*	Ishikari-wakasagi					*Hypomesus olidus*	*Hypomesus olidus*				
108	Plecoglossidae	*Plecoglossus altivelis altivelis*	Ayu					*Plecoglossus altivelis altivelis*	*Plecoglossus altivelis altivelis*				
109	Plecoglossidae	*Plecoglossus altivelis ryukyuensis*	Ryukyu-ayu					*Plecoglossus altivelis ryukyuensis*	*Plecoglossus altivelis ryukyuensis*				
110	Salmonidae	*Hucho perryi*	Itou					*Hucho perryi*	*Hucho perryi*				
111	Salmonidae	*Salvelinus malma krascheninnikovi*	Oshorokoma					*Salvelinus malma krascheninnikovi*	*Salvelinus malma malma*				
112	Salmonidae	*Salvelinus malma miyabei*	Miyabe-iwana					*Salvelinus malma miyabei*	*Salvelinus malma miyabei*				
113	Salmonidae	*Salvelinus leucomaenis leucomaenis*	Amemasu					*Salvelinus leucomaenis leucomaenis*	*Salvelinus leucomaenis leucomaenis*				
114	Salmonidae	*Salvelinus leucomaenis japonicus*	Yamato-iwana					*Salvelinus leucomaenis japonicus*	*Salvelinus leucomaenis japonicus*				
115	Salmonidae	*Salvelinus leucomaenis pluvius*	Nikko-iwana					*Salvelinus leucomaenis pluvius*	*Salvelinus leucomaenis pluvius*				
116	Salmonidae	*Salvelinus leucomaenis imbrius*	Gogi					*Salvelinus leucomaenis imbrius*	*Salvelinus leucomaenis imbrius*				
117	Salmonidae	*Oncorhynchus keta*	Sake					*Oncorhynchus keta*	*Oncorhynchus keta*				
118	Salmonidae	*Oncorhynchus nerka nerka*	Himemasu					*Oncorhynchus nerka nerka*	*Oncorhynchus nerka nerka*				
119	Salmonidae	*Oncorhynchus kawamurae*	Kunimasu					*Oncorhynchus kawamurae*	*Oncorhynchus nerka kawamurae*				
120	Salmonidae	*Oncorhynchus gorbuscha*	Karafutomasu					*Oncorhynchus gorbuscha*	*Oncorhynchus gorbuscha*				
121	Salmonidae	*Oncorhynchus masou masou*	Sakuramasu/Yamame					*Oncorhynchus masou masou*	*Oncorhynchus masou masou*				
122	Salmonidae	*Oncorhynchus masou ishikawae*	Satsukimasu/Amago					*Oncorhynchus masou ishikawae*	*Oncorhynchus masou ishikawae*				

(continued)

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123	Salmonidae	*Oncorhynchus* sp.	Biwamasu		1		1	*Oncorhynchus* sp.	*Oncorhynchus masou* subsp.				Oohara and Okazaki (1996), Gwo et al. (2008) and Takahashi et al. (2015)
124	Gasterosteidae	*Gasterosteus nipponicus*	Nihon-itoyo					*Gasterosteus* sp.	*Gasterosteus aculeatus*	*Gasterosteus nipponicus* Higuchi et al. (2014)	1		Higuchi and Goto (1996)
125	Gasterosteidae	*Gasterosteus aculeatus aculeatus*	Itoyo	1	4	3		*Gasterosteus aculeatus aculeatus*	*Gasterosteus aculeatus*			Anadromous, Freshwater “Fukui”, “Aizu”, “Nasu”	Higuchi et al. (1996), Yamada et al. (2001) and Watanabe et al. (2003, unpublished data)
126	Gasterosteidae	*Gasterosteus aculeatus* subsp. 2	Hariyo	1	2	1	1	*Gasterosteus aculeatus* subsp. 2	*Gasterosteus microcephalus*			Hariyo “Nobi”, “Oumi”	Yamada et al. (2001) and Watanabe et al. (2003)
127	Gasterosteidae	*Pungitius tymensis*	Ezo-tomiyo					*Pungitius tymensis*	*Pungitius tymensis*				
128	Gasterosteidae	*Pungitius kaibarae*	Minami-tomiyo					*Pungitius kaibarae*	*Pungitius kaibarae*				
129	Gasterosteidae	*Pungitius* sp. 1	Tomiyo “Tansui-gata”		1		1	*Pungitius* sp. 1	*Pungitius sinensis*/ *Pungitius pungitius*			See footnote (a)	Takahashi et al. (2001) and Takahashi and Goto (2001)
130	Gasterosteidae	*Pungitius* sp. 2	Tomiyo “Kisui-gata”		1		1	*Pungitius* sp. 2	*Pungitius pungitius*			See footnote (a)	Takahashi et al. (2001) and Takahashi and Goto (2001)
131	Gasterosteidae	*Pungitius* sp. 3	Timiyo “Omono-gata”		1		1	*Pungitius* sp. 3	*Pungitius sinensis*/ *Pungitius pungitius*			See footnote (a)	Takahashi et al. (2001) and Takahashi and Goto (2001)
132	Gasterosteidae	*Pungitius* sp. 4	Musashi-tomiyo		1		1	*Pungitius* sp. 4	*Pungitius* sp.			See footnote (a)	Takahashi and Goto (2001)
133	Adrianichthyidae	*Oryzias latipes*	Minami-medaka					*Oryzias latipes*	*Oryzias latipes*				
134	Adrianichthyidae	*Oryzias sakaizumii*	Kitano-medaka					*Oryzias sakaizumii*	*Oryzias latipes*		1		Takehana et al. (2003)
135	Sinipercidae	*Coreoperca kawamebari*	Oyanirami	1	2	1		*Coreoperca kawamebari*	*Coreoperca kawamebari*			Two regional groups have been known, but not yet published	Takahashi et al. (unpublished data)
136	Cottidae	*Trachidermus fasciatus*	Yamanokami					*Trachidermus fasciatus*	*Trachidermus fasciatus*				
137	Cottidae	*Cottus kazika*	Ayukake					*Cottus kazika*	*Cottus kazika*				
138	Cottidae	*Cottus pollux*	Kajika					*Cottus pollux*	*Cottus pollux*				
139	Cottidae	*Cottus* sp.	Kajika “Churan-gata”		1		1	*Cottus pollux*					
140	Cottidae	*Cottus reinii*	Utsusemi-kajika		2	1		*Cottus reinii*	*Cottus reinii*			Utsusemikajika “Amphidromous”, “Lake Biwa”	Yokoyama and Goto (2005), Yokoyama and Yamamoto (2012) and Tabata et al. (2016)

141	Cottidae	*Cottus hangiongensis*	Kankyo-kajika					*Cottus hangiongensis*	*Cottus hangiongensis*				
142	Cottidae	*Cottus amblystomopsis*	Ezohana-kajika					*Cottus amblystomopsis*	*Cottus amblystomopsis*				
143	Cottidae	*Cottus nozawae*	Hana-kajika		3	2		*Cottus nozawae*	*Cottus nozawae*			Hana-kajika “Hokkaido”, “North Tohoku”, “Yamagata”	Yagami et al. (2002) and Yokoyama and Goto (2002)
144	Odontobutidae	*Odontobutis obscura*	Donko		4	3		*Odontobutis obscura*	*Odontobutis obscura*			Donko “West Kyushu”, “West Seto”, “East Seto”, “San’in–Biwa–Ise”	Sakai et al. (1998) and Mukai and Nishida (2003)
145	Odontobutidae	*Odontobutis hikimius*	Ishi-donko					*Odontobutis hikimius*	*Odontobutis hikimius*		1		Sakai et al. (1998) and Mukai and Nishida (2003)
146	Eleotrididae	*Hypseleotris cyprinoides*	Tanagomodoki					*Hypseleotris cyprinoides*	*Hypseleotris cyprinoides*				
147	Eleotrididae	*Eleotris oxycephala*	Kawaanago					*Eleotris oxycephala*	*Eleotris oxycephala*				
148	Eleotrididae	*Eleotris fusca*	Tenjiku-kawaanago					*Eleotris fusca*	*Eleotris fusca*				
149	Eleotrididae	*Ophieleotris* sp. 1	Tametomohaze		1		1	*Ophieleotris* sp. 1	*Ophieleotris* sp.				
150	Eleotrididae	*Ophieleotris* sp. 2	Goshiki-tametomohaze		1		1	*Ophieleotris* sp. 2					
151	Gobiidae	*Luciogobius albus*	Dokutsu−mimizuhaze					*Luciogobius albus*					
152	Gobiidae	*Luciogobio fluvialis*	Nagare-mimizuhaze					*Luciogobio fluvialis*			1		
153	Gobiidae	*Luciogobio fonticola*	Yuusui-mimizuhaze					*Luciogobio fonticola*			1		
154	Gobiidae	*Sicyopterus japonicus*	Bouzuhaze					*Sicyopterus japonicus*	*Sicyopterus japonicus*				
155	Gobiidae	*Stiphodon percnopterygionus*	Nanyo-bouzuhaze					*Stiphodon percnopterygionus*	*Stiphodon percnopterygionus*				
156	Gobiidae	*Stiphodon atropurpureus*	Konteri-bouzuhaze					*Stiphodon atropurpureus*					
157	Gobiidae	*Stenogobius* sp.	Tanekawa-haze		1		1	*Stenogobius* sp.					
158	Gobiidae	*Awaous melanocephalus*	Kuro-minamihaze					*Awaous melanocephalus*	*Awaous melanocephalus*				
159	Gobiidae	*Tridentiger brevispinis*	Numa-chichibu					*Tridentiger brevispinis*	*Tridentiger brevispinis*				
160	Gobiidae	*Rhinogobius flumineus*	Kawa-yoshinobori		≥ 3	2		*Rhinogobius flumineus*	*Rhinogobius flumineus*			Five groups are recognized, and at least three regional groups may exist	Masuda et al. (1989), Shimuzu T et al. (1993) and Mukai et al. (2005)
161	Gobiidae	*Rhinogobius nagoyae*	Shima-yoshinobori					*Rhinogobius nagoyae*	*Rhinogobius* sp. CB				Masuda et al. (1989), Mukai et al. (2005) and Yamasaki et al. (2015)
162	Gobiidae	*Rhinogobius* sp. CO	Ruri-yoshinobori		1		1	*Rhinogobius* sp. CO	*Rhinogobius* sp. CO				Masuda et al. (1989), Mukai et al. (2005) and Yamasaki et al. (2015)

(continued)

ID	Family	Scientific name	Japanese common name	Unpublished	Undescribed/ undetermined	Increment	Un-named	Nakabo (2013)	Kawanabe et al. (2001)	Described after, or not included in Nakabo (2013)	Described in and after 2000	Tentative name	Reference(s) relating to cryptic lineages
163	Gobiidae	*Rhinogobius fluviatilis*	Oo-yoshinobori					*Rhinogobius fluviatilis*	*Rhinogobius* sp. LD				Masuda et al. (1989), Mukai et al. (2005) and Yamasaki et al. (2015)
164	Gobiidae	*Rhinogobius brunneus*	Kuro-yoshinobori					*Rhinogobius brunneus*	*Rhinogobius* sp. DA				Masuda et al. (1989), Mukai et al. (2005) and Yamasaki et al. (2015)
165	Gobiidae	*Rhinogobius giurinus*	Gokurakuhaze					*Rhinogobius giurinus*	*Rhinogobius giurinus*				Masuda et al. (1989), Mukai et al. (2005) and Yamasaki et al. (2015)
166	Gobiidae	*Rhinogobius* sp. TO	Tokai-yoshinobori		1		1	*Rhinogobius* sp. TO					Yamasaki et al. (2015)
167	Gobiidae	*Rhinogobius kurodai*	Kuroda-haze					*Rhinogobius kurodai*					Ohara et al. (2009) and Yamasaki et al. (2015)
168	Gobiidae	*Rhinogobius* sp. BF	Shimahire-yoshinobori		1		1	*Rhinogobius* sp. BF					Ohara et al. (2009) and Yamasaki et al. (2015)
169	Gobiidae	*Rhinogobius* sp. BW	Biwa-yoshinobori		1		1	*Rhinogobius* sp. BW					Mukai et al. (2005), Takahashi and Okazaki (2002), Takahashi and Ohara (2004) and Yamasaki et al. (2015)
170	Gobiidae	*Rhinogobius* sp. KZ	Kazusa-yoshinobori		1		1	*Rhinogobius* sp. KZ					Masuda et al. (1989), Ohara et al. (2009) and Yamasaki et al. (2015)
171	Gobiidae	*Rhinogobius* sp. OM	Oumi-yoshinobori		1		1	*Rhinogobius* sp. OM					Masuda et al. (1989), Ohara et al. (2009) and Yamasaki et al. (2015)
172	Gobiidae	*Rhinogobius* sp. OR	"To-yoshinobori"		1		1		*Rhinogobius* sp. OR	There exist regional populations that are not included in Nakabo (2013)			Ohara et al. (2009) and Yamasaki et al. (2015)
173	Gobiidae	*Glossogobius aureus*	Konjikihaze					*Glossogobius aureus*	*Glossogobius aureus*				
174	Gobiidae	*Gymnogobius isaza*	Isaza					*Gymnogobius isaza*	*Gymnogobius isaza*				
175	Gobiidae	*Gymnogobius petschiliensis*	Sumi-ukigori					*Gymnogobius petschiliensis*	*Gymnogobius* sp. 2				
176	Gobiidae	*Gymnogobius urotaenia*	Ukigori					*Gymnogobius urotaenia*	*Gymnogobius urotaenia*				
177	Gobiidae	*Gymnogobius opperiens*	Shima-ukigori					*Gymnogobius opperiens*	*Gymnogobius* sp. 1				
178	Gobiidae	*Gymnogobius castaneus*	Juzukakehaze					*Gymnogobius castaneus*	*Gymnogobius laevis*			"Widely-distributed species" in Mukai et al. (2010)	Aizawa et al. (1994), Sota et al. (2005) and Chiba et al. (2015)

179	Gobiidae	*Gymnogobius nakamurae*	Koshinohaze					*Gymnogobius nakamurae*				"Chokai-endemic species" in Mukai et al. (2010)	Aizawa et al. (1994), Sota et al. (2005) and Chiba et al. (2015)
180	Gobiidae	*Gymnogobius* sp. 1	Musashino-juzukakehaze		1		1	*Gymnogobius* sp. 1				"Kanto-endemic species" in Mukai et al. (2010)	Aizawa et al. (1994), Sota et al. (2005) and Chiba et al. (2015)
181	Gobiidae	*Gymnogobius* sp. 2	Hokuriku-juzukakehaze		1		1					"Toyama-endemic species" in Mukai et al. (2010)	Aizawa et al. (1994), Sota et al. (2005) and Chiba et al. (2015)

Total of "known" taxa: 181

Unnamed taxa: 31 (17.1 %)

Potential increments of "evolutionary units": +63

Potential total number of "evolutionary units": 244

[a] The list and counts do not include the taxa that were described or determined after September 2015; please see Nakajima (2016) for ID 79 and Takahashi et al. (2016) for IDs 129–132

Data Source for Appendix 4

Abe T, Kobayashi I, Watanabe K (2013) An extant native population of the Japanese rosy bitterling, *Rhodeus ocellatus kurumeus*, in the Sanyo Region, western Japan. Jpn J Ichthyol 60:49–55

Aiki H, Takayama K, Tamaru T, Mano N, Shimada M, Komaki H, Hirose H (2009) Phylogeography of the Japanese eight-barbel loach *Lefua echigonia* from the Yamagata area of the Tohoku district, Japan. Fish Sci 7:903–908

Aizawa T, Hatsumi M, Wakahama K (1994) Systematic study on the *Chaenogobius* species (family Gobiidae) by analysis of allozyme polymorphisms. Zool Sci 11:455–465

Chiba SN, Kakehashi R, Shibukawa K, Mukai T, Suzuki Y, Hanzawa N (2015) Geographical distribution and genetic diversity of *Gymnogobius* sp. 'Chokai-endemic species' (Perciformes: Gobiidae). Ichthyol Res 62:156–162

Gwo JC, Hsu TH, Lin KH, Chou YC (2008) Genetic relationship among four subspecies of cherry salmon (*Oncorhynchus masou*) inferred using AFLP. Mol Phylogenet Evol 48:776–781

Hashiguchi Y, Kado T, Kimura S, Tachida H (2006) Comparative phylogeography of two bitterlings, *Tanakia lanceolata* and *T. limbata* (Teleostei, Cyprinidae), in Kyushu and adjacent districts of western Japan, based on mitochondrial DNA analysis. Zool Sci 23:309–322

Higuchi M, Goto A (1996) Genetic evidence supporting the existence of two distinct species in the genus *Gasterosteus* around Japan. Environ Biol Fish 47:1–16

Higuchi M, Sakai H, Goto A (2014) A new threespine stickleback, *Gasterosteus nipponicus* sp. nov. (Teleostei: Gasterosteidae), from the Japan Sea region. Ichthyol Res 61:341–351

Kakioka R, Kokita T, Tabata R, Mori S, Watanabe K (2013) The origins of limnetic forms and cryptic divergence in *Gnathopogon* fishes (Cyprinidae) in Japan. Environ Biol Fish 96:631–644

Kano Y, Watanabe K, Nishida S, Kakioka R, Wood C, Shimatani Y, Kawaguchi Y (2011) Population genetic structure, diversity and stocking effect of the oriental weatherloach (*Misgurnus anguillicaudatus*) in an isolated island. Environ Biol Fish 90:211–222

Kawanabe H, Mizuno N, Hosoya K (2001) Freshwater fishes of Japan, 3rd edn. Yama-Kei, Tokyo

Kawase S, Hosoya K (2015) *Pseudorasbora pugnax*, a new species of minnow from Japan, and redescription of *P. pumila* (Teleostei: Cyprinidae). Ichthyol Explor Freshw 25:289–298

Kitagawa T, Yoshioka M, Kashiwagi M, Okazaki T (2001a) Population structure and local differentiation in the delicate loach, *Niwaella delicata*, as revealed by mitochondrial DNA and morphological analyses. Ichthyol Res 48:127–135

Kitagawa T, Watanabe M, Kobayashi T, Yoshioka M, Kashiwagi N, Okazaki T (2001b) Two genetically divergent groups in the Japanese spined loach, *Cobitis takatsuensis*, and their phylogenetic relationships among Japanese *Cobitis* inferred from mitochondrial DNA analyses. Zool Sci 18:249–259

Kitagawa T, Watanabe M, Kitagawa E, Yoshioka M, Kashiwagi M, Okazaki T (2003) Phylogeography and the maternal origin of the tetraploid form of the Japanese spined loach, *Cobitis biwae*, revealed by mitochondrial DNA analysis. Ichthyol Res 50:318–325

Kitagawa T, Jeon SR, Kitagawa E, Yoshioka M, Kashiwagi M, Okazaki T (2005) Genetic relationships among the Japanese and Korean striated spined loach complex (Cobitidae: *Cobitis*) and their phylogenetic positions. Ichthyol Res 52:111–122

Kitagawa E, Nakajima J, Hoshino K, Kitagawa T (2009) Geographic distribution and biogeographical origin of the spined loach genus *Cobitis* in north-eastern Kyushu Island, Japan. Jpn J Ichthyol 56:7–19

Kitagawa T, Fujii Y, Koizumi N (2011) Origin of the two major distinct mtDNA clades of the Japanese population of the oriental weather loach *Misgurnus anguillicaudatus* (Teleostei: Cobitidae). Folia Zool 60:343–349

Kitamura J, Nagata N, Nakajima J, Sota T (2012) Divergence of ovipositor length and egg shape in a brood parasitic bitterling fish through the use of different mussel hosts. J Evol Biol 25:566–573

Kitanishi S, Nishio M, Uehara K, Ogawa R, Yokoyama T, Edo K (2013) Patterns of genetic diversity of mitochondrial DNA within captive populations of the endangered Itasenpara bitterling: implications for a reintroduction program. Environ Biol Fish 96:567–572

Kitanishi S, Hayakawa A, Takamura K, Nakajima J, Kawaguchi Y, Onikura N, Mukai T (2016) Phylogeography of *Opsariichthys platypus* in Japan based on mitochondrial DNA sequences. Ichthyol Res. doi:10.1007/s10228-016-0522-y

Kitazima J, Matsuda M, Mori S, Kokita T, Watanabe K (2015) Population structure and cryptic replacement of local populations in the endangered bitterling *Acheilognathus cyanostigma*. Ichthyol Res 62:122–130

Kobayashi T (2008) Genetic characteristics of local populations of the fluvial eight-barbel loach *Lefua* sp., in Tottori and Okayama Prefectures. Nat Environ Sci Res (Hiraoka Environmental Science Laboratory) 21:37–42

Koizumi N, Takemura T, Watabe K, Mori A (2009) Genetic variation and diversity of Japanese loach inferred from mitochondrial DNA–phylogenetic analysis using the cytochrome *b* gene sequences. Trans JSIDRE (259):7–16

Komiya T, Fujita-Yanahibayashi S, Watanabe K (2014) Multiple colonizations of Lake Biwa by *Sarcocheilichthys* fishes and their population history. Environ Biol Fish 97:741–755

Kottelat M (2012) Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidei). Raffles Bull Zool Suppl (26):1–199

Mabuchi K, Senou H, Suzuki T, Nishida M (2005) Discovery of an ancient lineage of *Cyprinus carpio* from Lake Biwa, central Japan, based on mtDNA sequence data, with reference to possible multiple origins of koi. J Fish Biol 66:1516–1528

Mabuchi K, Seno H, Nishida M (2008) Mitochondrial DNA analysis reveals cryptic large-scale invasion of non-native genotypes of common carp (*Cyprinus carpio*) in Japan. Mol Ecol 17: 796–809

Masuda Y, Ozawa T, Enami S (1989) Genetic differentiation among eight color types of the freshwater goby, *Rhinogobius brunneus*, from western Japan. Jpn J Ichthyol 36:30–41

Matsuba H, Yoshimi S, Inoue M, Hata H (2014) Origin of *Tanakia limbata* in Ehime Prefecture indicated by phylogeographic analysis of mitochondrial cytochrome *b* gene sequences Jpn J Ichthyol 61:89–96

Mihara M, Sakai T, Nakao K, Martins LD, Hosoya K, Miyazaki J (2005) Phylogeography of loaches of the genus *Lefua* (Balitoridae, Cypriniformes) inferred from mitochondrial DNA sequences. Zool Sci 22:157–168

Miyake T, Nakajima J, Onikura N, Ikemoto S, Iguchi K, Komaru A, Kawamura K (2011) The genetic status of two subspecies of *Rhodeus atremius*, an endangered bitterling in Japan. Conserv Genet 12:383–400

Miyazaki J, Nakao K, Mihara M, Sakai T, Gunji Y, Tojo K, Muraoka K, Hosoya K (2007) Incongruence between mtDNA phylogeny and morphologial [morphological] and ecological characters in loaches of the genus *Lefua* (Balitoridae, Cypriniformes). Zool Sci 24:666–675

Miyazaki J, Dobashi M, Tamura T, Beppu S, Sakai T, Mihara M, Hosoya K (2011) Parallel evolution in eight-barbel loaches of the genus *Lefua* (Balitoridae, Cypriniformes) revealed by mitochondrial and nuclear DNA phylogenies. Mol Phylogenet Evol 60:416–427

Morishima K, Shiokawa YN, Bando E, Li YJ, Boron A, Khan MMR, Arai K (2008) Cryptic clonal lineages and genetic diversity in the loach *Misgurnus anguillicaudatus* (Teleostei: Cobitidae) inferred from nuclear and mitochondrial DNA analyses. Genetica 132:159–171

Mukai T, Nishida M (2003) Mitochondrial DNA phylogeny of Japanese freshwater goby, *Odontobutis obscura*, and an evidence for artificial transportation to Kanto District. Jpn J Ichthylol 50:71–76

Mukai T, Nakamura S, Suzuki T, Nishida M (2005) Mitochondrial DNA divergence in yoshinobori gobies (*Rhinogobius* species complex) between the Bonin Islands and the Japan–Ryukyu Archipelago. Ichthyol Res 52:410–413

Mukai T, Shibukawa K, Shinozaki T, Sugiyama H, Chiba SN, Hanzawa N (2010) Preliminary review and conservation of *Gymnogobius castaneus* complex in Japan. Jpn J Ichthyol 57:173–176

Nakabo (2013) Fishes of Japan with pictorial keys to the species, 3rd edn. Tokai University Press, Tokyo

Nakagawa H, Seki S, Ishikawa T, Watanabe K (2016) Genetic population structure of the Japanese torrent catfish *Liobagrus reinii* (Amblycipitidae), inferred from mitochondrial cytochrome *b* variations. Ichthyol Res 63:333–346

Nakajima J (2012) Taxonomic study of the *Cobitis striata* complex (Cypriniformes, Cobitidae) in Japan. Zootaxa 3586:103–130

Nakajima J (2016) *Cobitis takenoi* sp. n. (Cypriniformes, Cobitidae): a new spined loach from Honshu Island, Japan. ZooKeys 568:119–128

Nakajima J, Nakamura T, Suzawa Y (2011) Record of peculiar *Cobitis* (Cypriniformes: Cobitidae) from the Oyodo River system in Miyazaki Prefecture, southern Kyushu Island, Japan. Jpn J Ichthyol 58:153–160

Nakajima J, Suzawa Y (2015) *Cobitis sakahoko*, a new species of spined loach (Cypriniformes: Cobitidae) from southern Kyushu Island, Japan. Ichthyol Res doi:10.1007/s10228-015-0476-5

Nakajima J, Suzuwa Y, Shimizu T, Saitoh K (2012) Proposal of standard Japanese names for Japanese loaches in the genus *Cobitis* (Cobitidae). Jpn J Ichthyol 59:86–95

Ohara K, Hotta M, Takahashi D, Asahida T, Ida H, Umino T (2009) Use of microsatellite DNA and otolith Sr:Ca ratios to infer genetic relationships and migration history of four morphotypes of *Rhinogobius* sp. OR. Ichthyol Res 56:373–379

Okazaki T, Watanabe M, Inamura O, Kitagawa T, Tabe M, Nagata Y (2006) Genetic relationships among regional populations of the deepbodied bitterling, *Acheilognathus longipinnis*, inferred from mitochondrial DNA analysis. DNA Polymorphism 14:276–280

Oohara I, Okazaki T (1996) Genetic relationship among three subspecies of *Oncorhynchus masou* determined by mitochondrial DNA sequence analysis. Zool Sci 13:189–198

Perdices A, Vasil'ev V, Vasil'eva E (2012) Molecular phylogeny and intraspecific structure of loaches (genera *Cobitis* and *Misgurnus*) from the Far East region of Russia and some conclusions on their systematics. Ichthyol Res 59:113–123

Saitoh K, Kobayashi T, Ueshima R, Numachi K (2000) Analyses of mitochondrial and satellite DNAs on spined loaches of the genus *Cobitis* from Japan have revealed relationships among populations of three diploid–tetraploid complexes. Folia Zool 49:9–16

Saitoh K, Chen WJ, Mayden RL (2010) Extensive hybridization and tetrapolyploidy in spined loach fish. Mol Phylogenet Evol 56:1001–1010

Saka R, Takehana Y, Suguro N, Sakaizumi M (2003) Genetic population structure of *Lefua echigonia* inferred from allozymic and mitochondrial cytochrome *b* variations. Ichthyol Res 50:140–148

Sakai H, Amano S (2014) A new subspecies of anadromous Far Eastern dace, *Tribolodon brandtii maruta* subsp. nov. (Teleostei, Cyprinidae) from Japan. Bull Natl Mus Nat Sci Ser A 40:219–229

Sakai H, Yamamoto C, Iwata A (1998) Genetic divergence, variation and zoogeography of a freshwater goby, *Odontobutis obscura*. Ichthyol Res 45:363–376

Sakai H, Goto A, Jeon SR (2002) Speciation and dispersal of *Tribolodon* species (Pisces, Cyprinidae) around the Sea of Japan. Zool Sci 19:1291–1303

Sakai T, Mihara M, Shitara H, Yonekawa H, Hosoya K, Miyazaki J (2003) Phylogenetic relationships and intraspecific variations of loaches of the genus *Lefua* (Balitoridae, Cypriniformes). Zool Sci 20:501–514

Sasaki T, Kartavtsev YP, Chiba SN, Uematsu T, Sviridov VV, Hanzawa N (2007) Genetic divergence and phylogenetic independence of Far Eastern species in subfamily Leuciscinae (Pisces: Cyprinidae) inferred from mitochondrial DNA analyses. Genes Genet Syst 82:329–340

Shimizu T, Taniguchi N, Mizuno N (1993) An electrophoretic study of genetic differentiation of a Japanese freshwater goby, *Rhinogobius flumineus*. Jpn J Ichthyol 39:329–343

Shimizu T, Suzawa Y, Sakai H (2004) Allozyme divergence between two groups of the Japanese spinous loach, *Cobitis takatsuensis*. Ichthyol Res 51:241–247

Shimizu T, Suzuki T, Takagi M, Oseko N (2011) Morphological and genetic characteristics of misgurnid loach from Okinawa and Iriomote Islands. Bull Biogeogr Soc Jpn 66:141–153

Shimizu Y, Oshiro T, Sakaizumi M (1993) Electrophoretic studies of diploid, triploid, and tetraploid forms of the Japanese silver carp, *Carassius auratus langsdorfii*. Jpn J Ichthyol 40:65–75

Sota T, Mukai T, Shinozaki T, Sato H, Yodoe K (2005) Genetic differentiation of the gobies *Gymnogobius castaneus* and *G. taranetzi* in the region surrounding the Sea of Japan as inferred from a mitochondrial gene genealogy. Zool Sci 22:87–93

Stieler P (1907) *Barilius neglectus* sp.n. Blätter für Aquarien- und Terrarien-Kunde Stuttgart 18 (17):169

Tabata R, Kakioka R, Tominaga K, Komiya T, Watanabe K (2016) Phylogeny and historical demography of endemic fishes in Lake Biwa: the ancient lake as a promoter of evolution and diversification of freshwater fishes in western Japan. Ecol Evol 6:2601–2623

Takada M, Tachihara K, Kon T, Yamamoto G, Iguchi K, Miya M, Nishida M (2010) Biogeography and evolution of the *Carassius auratus*-complex in East Asia. BMC Evol Biol 10:1–18

Takahashi D, Ohara K (2004) Genetic variations estimated from PCR-RFLP analysis of two morphs of the freshwater goby *Rhinogobius* in the Lake Biwa water system. Ichthyol Res 51:99–105

Takahashi H, Goto A (2001) Evolution of East Asian ninespine sticklebacks as shown by mitochondrial DNA control region sequences. Mol Phylogenet Evol 21:135–155

Takahashi H, Takata K, Goto A (2001) Phylogeography of lateral plate dimorphism in the freshwater type of ninespine sticklebacks, genus *Pungitius*. Ichthyol Res 48:143–154

Takahashi H, Kondou T, Takeshita N, Hsu TH, Nishida M (2015) Evolutionary process of iwame, a markless form of the red-spotted masu salmon *Oncorhynchus masou ishikawae*, in the Ôno River, Kyushu. Ichthyol Res doi:10.1007/s10228-015-0482-7

Takahashi H, Møller PR, Shedko SV, Ramatulla T, Joen SR, Zhang CG, Sideleva VG, Takata K, Sakai H, Goto A, Nishida M (2016) Species phylogeny and diversification process of Northeast Asian *Pungitius* revealed by AFLP and mtDNA markers. Mol Phylogenet Evol 99:44–52

Takahashi S, Okazaki T (2002) A new lentic form of the "*yoshinobori*" species complex, *Rhinogobius* spp. from Lake Biwa, Japan, compared with lake-river migrating *Rhinogobius* sp. OR. Ichthyol Res 49:333–339

Takehana Y, Nagai N, Matsuda M, Tsuchiya K, Sakaizumi M (2003) Geographic variation and diversity of the cytochrome *b* gene in Japanese wild populations of medaka, *Oryzias latipes*. Zool Sci 20:1279–1291

Takeno M, Kashiwagi S, Kitagawa T (2010) A distinctive allotetraploid spined loach population (genus *Cobitis*) from Tango District, Kyoto Prefecture, Japan. Jpn J Ichthyol 57:105–112

Takeuchi M, Isono M, Hida S, Maki N, Onikubo H, Miyazaki JI (2015) Phylogenetic position of Japanese right-barbel loach *Lefua echigonia* (Balitoridae, Cypriniformes) discovered in Iwate Prefecture, Japan. J Nat Hist Aomori (20):79–80

Tominaga K, Nakajima J, Watanabe K (2016) Cryptic divergence and phylogeography of the pike gudgeon *Pseudogobio esocinus* (Teleostei: Cyprinidae): a comprehensive case of freshwater phylogeography in Japan. Ichthyol Res 63:79–93

Watanabe K, Iguchi K, Hosoya K, Nishida M (2000) Phylogenetic relationships of the Japanese minnows, *Pseudorasbora* (Cyprinidae), as inferred from mitochondrial 16S rRNA gene sequences. Ichthyol Res 47:43–50

Watanabe K, Kawase S, Mukai T, Kakioka R, Miyazaki J-I, Hosoya K (2010) Population divergence of *Biwia zezera* (Cyprinidae: Gobioninae) and the discovery of a cryptic species, based on mitochondrial and nuclear DNA sequence analyses. Zool Sci 27:647–655

Watanabe K, Mori S (2008) Comparison of genetic population structure between two cyprinids, *Hemigrammocypris rasborella* and *Pseudorasbora pumila* subsp., in the Ise Bay basin, central Honshu, Japan. Ichthyol Res 55:309–320 (Errata: Ichthyol Res 56:108)

Watanabe K, Mori S, Nishida M (2003) Genetic relationships and origin of two geographic groups of the freshwater threespine stickleback, 'Hariyo.' Zool Sci 20:265–274

Watanabe K, Mori S, Tanaka T, Kanagawa N, Itai T, Kitamura J, Suzuki N, Tominaga K, Kakioka R, Tabata R, Abe T, Tashiro Y, Hashimoto Y, Nakajima J, Onikura N (2014) Genetic population structure of *Hemigrammocypris rasborella* (Cyprinidae) inferred from mtDNA sequences. Ichthyol Res 61:352–360

Yagami T, Yokoyama R, Goto A (2002) Genetic fragmentation of populations of the fluvial sculpin *Cottus nozawae* (Pisces: Cottidae) at the southern margin of its native range. Can J Zool 80:873–881

Yamada M, Higuchi M, Goto A (2001) Extensive introgression of mitochondrial DNA found between two genetically divergent forms of threespine stickleback, *Gasterosteus aculeatus*, around Japan. Environ Biol Fish 61:269–284

Yamasaki YY, Nishida M, Suzuki T, Mukai T, Watanabe K (2015) Phylogeny, hybridization, and life history evolution of *Rhinogobius* gobies in Japan, inferred from multiple nuclear gene sequences. Mol Phylogenet Evol 90:20–33

Yamazaki Y, Goto A (1996) Genetic differentiation of *Lethenteron reissneri* populations, with reference to the existence of discrete taxonomic entities. Ichthyol Res 43:283–299

Yamazaki Y, Goto A (1998) Genetic structure and differentiation of four *Lethenteron* taxa from the Far East, deduced from allozyme analysis. Environ Biol Fish 52:149–161

Yamazaki Y, Goto A, Nishida M (2003) Mitochondrial DNA sequence divergence between two cryptic species of *Lethenteron*, with reference to an improved identification technique. J Fish Biol 62:591–609

Yamazaki Y, Yokoyama R, Nishida M, Goto A (2006) Taxonomy and molecular phylogeny of *Lethenteron* lampreys in eastern Eurasia. J Fish Biol 68(suppl B):251–269

Yokoyama R, Goto A (2002) Phylogeography of a freshwater sculpin, *Cottus nozawae*, from the northeastern part of Honshu Island, Japan. Ichthyol Res 49:147–155

Yokoyama R, Goto A (2005) Evolutionary history of freshwater sculpins, genus *Cottus* (Teleostei; Cottidae) and related taxa, as inferred from mitochondrial DNA phylogeny. Mol Phylogenet Evol 36:654–668

Yokoyama R, Yamamoto S (2012) Freshwater sculpin dwelling in Lake Chuzenji, Nikko, Kanto District, Japan, is identified as Utsusemikajika, *Cottus reinii*, unintentionally introduced from Lake Biwa. Ichthyol Res 59:389–393

Zarske A (2013) *Barilius neglectus* Stieler, 1907, ein senior synonym von *Hemigrammocypris rasborella* Fowler, 1910 (Teleostei: Cypriniformes: Cyprinidae). Vert Zool 63:253–257

References

Aoyagi H (1957) General notes on the freshwater fishes of the Japanese Archipelago. Taishukan, Tokyo

Avise JC (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge

Avise JC, Arnold J, Ball RM Jr, Bermingham E, Lamb T, Neigel JE, Reeb CA, Saunders NC (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annu Rev Ecol Syst 18:489–522

Ballard JWO, Whitlock MC (2004) The incomplete natural history of mitochondria. Mol Ecol 13:729–744

Bănărescu P (1990) Zoogeography of fresh waters, vol. 1: general distribution and dispersal of freshwater animals. AULA, Wiesbaden

Berra TM (2001) Freshwater fish distribution. Academic Press, San Diego

Brooks DR, van Veller MGP (2003) Critique of parsimony analysis of endemicity as a method of historical biogeography. J Biogeogr 30:819–825

Cheng P, Yu D, Liu S, Tang Q, Liu H (2014) Molecular phylogeny and conservation priorities of the subfamily Acheilognathinae (Teleostei: Cyprinidae). Zool Sci 31:300–308

Darlington PJ Jr (1957) Zoogeography: the geographical distribution of animals. Wiley, New York

Davey JW, Hohenlohe PA, Etter PD, Boone JQ, Catchen JM, Blaxter ML (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. Nat Rev Genet 12:499–510

Emerson KJ, Merz CR, Catchen JM, Hohenlohe PA, Cresko WA, Bradshaw WE, Holzapfel CM (2010) Resolving postglacial phylogeography using high-throughput sequencing. Proc Natl Acad Sci USA 107:16196–16200

Frankham R, Ballou JD, Briscoe DA (2002) Introduction to conservation genetics. Cambridge University Press, London

Goto A (1987) Freshwater fishes: their grouping by life history strategy and their distribution pattern. In: Mizuno N, Goto A (eds) Freshwater fishes in Japan: their distribution, variation and speciation. Tokai University Press, Tokyo, pp 1–15

Kakioka R, Kokita T, Tabata R, Mori S, Watanabe K (2013) The origins of limnetic forms and cryptic divergence in *Gnathopogon* fishes (Cyprinidae) in Japan. Environ Biol Fish 96:631–644

Kato H (1992) Fossa Magna—a masked border region separating southwest and northeast Japan. Bull Geol Surv Jpn 43:1–30

Kawabe T (1994) Biwako no Oitachi (formation of Lake Biwa). In: Research Group for Natural History of Lake Biwa (ed) Biwako no Shizenshi (The natural history of Lake Biwa). Yasaka Shobo, Tokyo, pp 24–72

Kawanabe H, Mizuno N, Hosoya K (2001) Freshwater fishes of Japan, 3rd edn. Yama-Kei Publishers, Tokyo

Kitagawa T, Watanabe M, Kitagawa E, Yoshioka M, Kashiwagi M, Okazaki T (2003) Phylogeography and the maternal origin of the tetraploid form of the Japanese spined loach, *Cobitis biwae*, revealed by mitochondrial DNA analysis. Ichthyol Res 50:318–325

Kitamura J, Nagata N, Nakajima J, Sota T (2012) Divergence of ovipositor length and egg shape in a brood parasitic bitterling fish through the use of different mussel hosts. J Evol Biol 25:566–573

Komiya T, Fujita-Yanagibayashi S, Watanabe K (2014) Multiple colonizations of Lake Biwa by *Sarcocheilichthys* fishes and their population history. Environ Biol Fish 97:741–755

Lévêque C, Oberdorff T, Paugy D, Stiassny MLJ, Tedescoet PA (2008) Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595:545–567

Lindberg GU (1972) Large-scale fluctuations of sea level in the Quaternary period: hypothesis based on biogeographical evidence. Nauka, Leningrad

Machida H, Matsuda T, Umitsu M, Koizumi T (2006) Regional geomorphology of the Japanese Islands, vol 5. Geomorphology of Chubu Region. University of Tokyo Press, Tokyo

McCormack JE, Hird SM, Zellmer AJ, Carstens BC, Brumfield RT (2013) Applications of next-generation sequencing to phylogeography and phylogenetics. Mol Phylogenet Evol 66:526–538

Miyazaki J, Dobashi M, Tamura T, Beppu S, Sakai T, Mihara M, Hosoya K (2011) Parallel evolution in eight-barbel loaches of the genus *Lefua* (Balitoridae, Cypriniformes) revealed by mitochondrial and nuclear DNA phylogenies. Mol Phylogenet Evol 60:416–427

Mizuno N (1987) Origin of Japanese freshwater fish fauna. In: Mizuno N, Goto A (eds) Freshwater fishes in Japan: their distribution, variation and speciation. Tokai University Press, Tokyo, pp 231–244

Mori T (1936) Studies on the geographical distribution of freshwater fishes in Eastern Asia. Keijo Imperial University, Keijo

Moritz C (1994) Defining 'Evolutionarily Significant Units' for conservation. Trends Ecol Evol 9:373–375

Morrone JJ, Crisci JV (1995) Historical biogeography: introduction to methods. Annu Rev Ecol Syst 26:373–401

Myers GS (1949) Salt tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijdr Dierkd 28:315–322

Nakabo T (2013) Fishes of Japan with pictorial keys to the species, 3rd edn. Tokai University Press, Tokyo

Nakagawa H, Seki S, Ishikawa T, Watanabe K (2016) Genetic population structure of the Japanese torrent catfish *Liobagrus reinii* (Amblycipitidae) inferred from mitochondrial cytochrome *b* variations. Ichthyol Res 63:333–346

Nakajima J, Onikura N, Matsui S, Oikawa S (2006) Geographical distribution of the genuine freshwater fishes in Fukuoka Prefecture, northern Kyushu, Japan. Jpn J Ichthyol 53:117–131

Nature Conservation Committee of the Ichthyological Society of Japan (2013) Domestic alien fishes: hidden threat to biodiversity. Tokai University Press, Hadano

Nishimura S (1974) Nihon-kai no seiritsu (Formation of the Sea of Japan). Tsukiji-Shokan, Tokyo

Rahel FJ (2000) Homogenization of fish faunas across the United States. Science 288:854–856

Ronquist F (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Syst Biol 46:195–203

Rosen BR (1988) From fossils to earth history: applied historical biogeography. In: Myers AA, Giller PS (eds) Analytical biogeography, an integrated approach to the study of animal and plant distributions. Chapman & Hall, London, pp 437–481

Rubinoff D, Holland BS (2005) Between two extremes: mitochondrial DNA is neither the panacea nor the nemesis of phylogenetic and taxonomic inference. Syst Biol 54:952–961

Sakai H, Yamamoto C, Iwata A (1998) Genetic divergence, variation and zoogeography of a freshwater goby, *Odontobutis obscura*. Ichthyol Res 45:363–376

Tabata R, Kakioka R, Tominaga K, Komiya T, Watanabe K (2016) Phylogeny and historical demography of endemic fishes in Lake Biwa: the ancient lake as a promoter of evolution and diversification of freshwater fishes in western Japan. Ecol Evol 6:2601–2623

Taranetz A (1936) Freshwater fishes of the basin of the northwestern part of the Japan Sea. Trans Inst Zool Acad Sci URSS 4:483–540

Tominaga K, Nakajima J, Watanabe K (2016) Cryptic divergence and phylogeography of the pike gudgeon *Pseudogobio esocinus* (Teleostei: Cyprinidae): a comprehensive case of freshwater phylogeography in Japan. Ichthyol Res 63:79–93

Watanabe K (1998) Parsimony analysis of the distribution pattern of Japanese primary freshwater fishes, and its application to the distribution of the bagrid catfishes. Ichthyol Res 45:259–270

Watanabe K (2012) Faunal structure of Japanese freshwater fishes and its artificial disturbance. Environ Biol Fish 94:533–547

Watanabe K (2013) Origin and diversification of freshwater fishes in Lake Biwa. In: Okuda N (ed) Biodiversity in aquatic systems and environments: in Lake Biwa. Springer, Tokyo

Watanabe K, Takahashi H (2010) Tansuigyorui chiri no shizenshi (Natural history of freshwater fish geography). Hokkaido University Press, Sapporo

Watanabe K, Takahashi H, Kitamura A, Yokoyama R, Kitagawa T, Takeshima H, Sato S, Yamamoto S, Takehana Y, Mukai T, Ohara K, Iguchi K (2006) Biogeographical history of Japanese freshwater fishes: phylogeographic approaches and perspectives. Jpn J Ichthyol 53:1–38

Watanabe K, Kano Y, Takahashi H, Mukai T, Kakioka R, Tominaga K (2010a) GEDIMAP: a database of genetic diversity for Japanese freshwater fishes. Ichthyol Res 57:107–109

Watanabe K, Kawase S, Mukai T, Kakioka R, Miyazaki J-I, Hosoya K (2010b) Population divergence of *Biwia zezera* (Cyprinidae: Gobioninae) and the discovery of a cryptic species, based on mitochondrial and nuclear DNA sequence analyses. Zool Sci 27:647–655

Watanabe K, Mori S, Tanaka T, Kanagawa N, Itai T, Kitamura J, Suzuki N, Tominaga T, Kakioka R, Tabata R, Abe T, Tashiro Y, Hashimoto Y, Nakajima J, Onikura N (2014) Genetic population structure of *Hemigrammocypris rasborella* (Cyprinidae) inferred from mtDNA sequences. Ichthyol Res 61:352–360

Xia X, Zhang X, Liu H (2005) Phylogeography and speciation of *Pseudogobio vaillanti* in China: deep molecular divergence in the absence of morphological change. Proc Natl Acad Sci USA 15:1064–1069

Yokoyama T (1988) Seinan Nihon no Shizenshi (Natural history of southwestern Japan). Sanwa-shobo, Tokyo

Yonekura N, Kaizuka S, Nogami M, Chinzai K (2001) Regional geomorphology of the Japanese Islands, vol. 1. Introduction to Japanese geomorphology. University of Tokyo Press, Tokyo

Chapter 8

The Species and Genetic Diversities of Insects in Japan, with Special Reference to the Aquatic Insects

Koji Tojo, Kazuki Sekiné, Tomoya Suzuki, Rie Saito, and Masaki Takenaka

Abstract Japan is often referred to as a global hotspot of biodiversity. With regard to species diversity, insects are no exception. To date, more than 30,000 insect species have been identified in Japan, and yet about 100,000 species of insects are considered to inhabit this country. In this chapter, we outline background factors contributing to the degree of diversification in the Japanese insect fauna. Of course, the high degree of Japan's insect diversity is perpetuated as a result of many complex factors. Among these factors, the humid Asian monsoon climate and the geography that stretches out from north to south are important. Furthermore, the relevance of the extremely complex geological history is believed to be especially important. In particular, the independent origin of northeastern and southwestern Japan from the Eurasian Continent must have also contributed greatly to the establishment of biodiversity. In view of these circumstances, we introduce several case studies focusing on aquatic insects with low dispersal ability. In addition, we investigate the phenomenon of genetic differentiation and species differentiation deeply associated with the geohistory of Japan. These selected species offer high potential to effectively investigate various evolutionary issues: that is, they are one of the typical 'key taxa' in terms of phylogeography and evolutionary biology.

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8.1 Introduction: Insect Fauna of Japan and Its Species Diversity

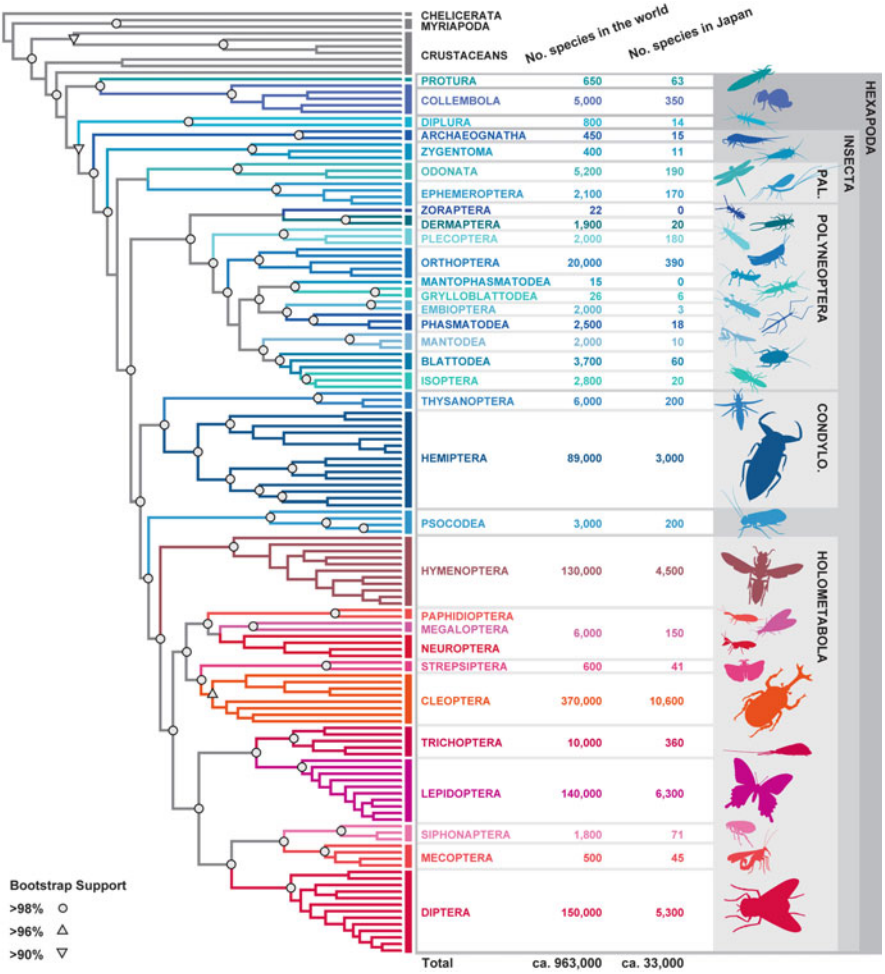
Japan consists of four major and numerous small islands, a total of 6,852, extending along the Pacific Coast of East Asia. Being less than 0.3 % of the land area of the world, the total land area of the archipelago is 378,000 km^2. However, a great variety of biota has been established for this archipelago albeit its limited land area. As such, the Japanese Archipelago is often referred to as a global hotspot of biodiversity. With regard to species diversity, insects are no exception.

To date, more than 33,000 insect species have been recorded from Japan (Fig. 8.1), and yet around 100,000 species of insects inhabit there. The establishment of such high diversity among Japanese insects can be attributed to various factors.

The approximate number of species in each insect order is shown in Fig. 8.1. There are only 2 insect orders among 32, Zoraptera and Mantophasmatodea, that have not yet been observed in Japan. It has become a great interest to us as to whether zorapteran insects will come to inhabit Japan, as they have been observed on Taiwan Island. Because extant species of Mantophasmatodea have been only found in arid regions in Central and Southern Africa, the possibility that they are found in Japan must be very small. Instead, the order Grylloblattodea is considered to be closely related to mantophasmatodeans, and is confined to the heavy snow and cool habitats of high-altitude mountains within East Asia and North America (i.e., the Japanese Archipelago, the Korean Peninsula, and the Rocky Mountains) straddling the Bering Strait (Schoville et al. 2013; Misof et al. 2014). In consideration of this unique situation, it is a mysterious and interesting subject to understand when and where the two lineages of mantophasmatodean and grylloblattodean insects were differentiated (Uchifune and Machida 2005).

8.1.1 Mechanisms of Establishment of Insect Diversity in Japan

With respect to the factors considered to have contributed to the species diversity of insects in Japan, one among others is the archipelago’s extensive habitat range in the north–south direction, which has provided a great contribution. The longitudinal range from end to end of Japan from Hokkaido to Okinawa (i.e., subarctic to subtropical climate zones) has been a critical factor facilitating the establishment of biodiversity in Japan. In addition, Japan also crosses an important biogeographic barrier, the Tokara Gap, dividing the Holarctic and Oriental Regions. This effect of



	No. species in the world	No. species in Japan
CHELICERATA		
MYRIAPODA		
CRUSTACEANS		
PROTURA	650	63
COLLEMBOLA	5,000	350
DIPLURA	800	14
ARCHAEOGNATHA	450	15
ZYGENTOMA	400	11
ODONATA	5,200	190
EPHEMEROPTERA	2,100	170
ZORAPTERA	22	0
DERMAPTERA	1,900	20
PLECOPTERA	2,000	180
ORTHOPTERA	20,000	390
MANTOPHASMATODEA	15	0
GRYLLOBLATTODEA	26	6
EMBIOPTERA	2,000	3
PHASMATODEA	2,500	18
MANTODEA	2,000	10
BLATTODEA	3,700	60
ISOPTERA	2,800	20
THYSANOPTERA	6,000	200
HEMIPTERA	89,000	3,000
PSOCODEA	3,000	200
HYMENOPTERA	130,000	4,500
PAPHIDIOPTERA	6,000	150
MEGALOPTERA		
NEUROPTERA		
STREPSIPTERA	600	41
CLEOPTERA	370,000	10,600
TRICHOPTERA	10,000	360
LEPIDOPTERA	140,000	6,300
SIPHONAPTERA	1,800	71
MECOPTERA	500	45
DIPTERA	150,000	5,300
Total	ca. 963,000	ca. 33,000

Fig. 8.1 Higher phylogenetic relationships of insects at the order level, and the approximate number of species of each order in the world and within Japan. This phylogenetic tree has been drawn based on the results estimated utilizing the meta-genome data sets produced from the transcriptome analyses of about 1500 genes by Misof et al. (2014). The phylogenetic tree in the original paper was inferred from a maximum-likelihood analysis of 413,459 amino acid sites divided into 479 meta-partitions. For information as to the number of species in each insect order, we referenced the following literature: Hirashima et al. (1989), Grimaldi and Engel (2005), Gullan and Cranston (2010), Cardé and Resh (2012), Ozono et al. (2012), etc. In the case of a discrepancy between these data sources, we adopted the most recently calculated species count. *CONDYLO* Condylognatha, *PAL* Palaeoptera

this barrier has also contributed greatly to the establishment of biodiversity. Furthermore, Japan is located at the eastern side of the Eurasian Continent and is strongly affected by the Asian monsoon climate. As a result, the Japanese Islands are under a wet and humid climate. Its geographic location and climate conditions have resulted in more than 70 % of Japan's land area having become covered in forests, and this also contributes greatly to facilitating the establishment of the rich biodiversity.

Another factor is its periods of connection to the continent. The resultant provision of a variety of dispersal routes must have also contributed greatly to the establishment of biodiversity, that is, the northern route (Hokkaido–Russian Primorye, Hokkaido–Sakhalin–Russian Primorye, and Hokkaido–Kuril Islands–Kamchatka Peninsula), the western route (Kyushu–Tsushima Island–Korean Peninsula), and the southwestern route (Kyushu–Ryukyu Islands–Taiwan–Chinese Mainland, Kyushu–Ryukyu Islands–Taiwan–Philippine Islands). In fact, many cases are known in which lineages had different routes and origins (e.g., northern and southern routes), and subsequently met on Japan.

8.1.2 Complex Formation History of the Japanese Islands

With respect to the diversity of insect fauna and their establishment mechanism in Japan, the relevance of location and climate conditions have already been mentioned in the previous section. However, the geological history of Japan is an important factor more than these climatic matters, because the Japanese Islands have an extremely complex formation history among the various geological regions of the world.

Almost all areas of Japan were originally attached to the eastern margin of the Eurasian Continent; that is, the Japanese Islands are mainly composed of elements of continental islands from which it originated. However, the Japanese Islands are also partially composed of elements of oceanic islands, such as in the Bonin and the Izu Islands.

Almost all areas of Japan were originally attached to the eastern margin of the Eurasian Continent until about 25 to 20 million years ago (Ma) (Fig. 8.2a). The subducting oceanic plates, being deeper than the continental plate, probably pulled the Japanese landmasses eastward, so opening up the Sea of Japan around 15 Ma (Barnes 2003).

As for the formation of the Japanese Archipelago, with respect to its separation from the Eurasian Continent, geologists suggested a 'dual origin' (or 'double-door-shaped opening') mode, such as the northeastern and southwestern portions of the Japanese Islands separated independently from the Eurasian Continent (Fig. 8.2b) (Otofuji et al. 1985). Such a double-door-shaped opening is probably peculiar to the geological phenomenon of the rifting of a continental fragment from a thick continental lithosphere (Otofuji et al. 1985). According to this theory, Sakhalin, central Hokkaido, and northern Honshu fragmented from the Far East Russian region during the spreading out of the Okhotsk Sea basin (Japan and Yamato basins), a little earlier than about 20 Ma. From then up until about 15 Ma, they also rotated approximately 47° counterclockwise, while southwestern Japan began to split, rotating away from the Korean Peninsula during the spreading out of the

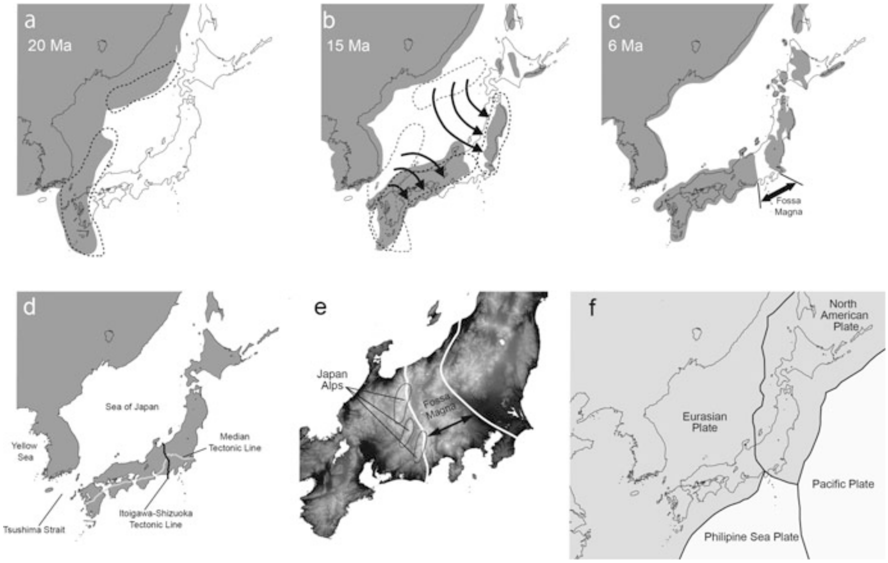


Fig. 8.2 Putative formation history of the Japanese Archipelago (after Otofuji et al. 1985; Seno et al. 1993; Ninomiya et al. 2014; Saito and Tojo 2016a, b). (**a**) The East Asian region as about 20 million years ago (20 Ma). The landmasses that later become the Proto-Japanese Islands were located along the eastern margin of the Eurasian Continent. (**b**) From around 15 MYA, the landmasses that formed the Proto-Japanese Islands began to separate from the Eurasian Continent. The northeastern and southwestern portions of the Japanese Islands separated independently from the continent. (**c**) By the point at which the landmasses of the Proto-Japanese Islands had substantially separated, northeastern and southwestern Japan remained separated by a sea zone called the Fossa Magna, during around 15–5 Ma. (**d**) Current map of the East Asian region. (**e**) Enlarged map of the central region of the current Japanese Islands. The Fossa Magna region of 15–5 Ma is indicated between the two *white lines*. (**f**) The geographic location of the boundaries of four major crustal plates under and around the Japanese Islands. Such an intersection of four major crustal plates is very rare, even globally

Tsushima basin. As such a 56° clockwise rotation continued up until about 15 Ma (Fig. 8.2b) (Otofuji et al. 1985).

It is considered that the most intense period of division and rotation occurred around 17–14 Ma (Hayashida et al. 1991; Otofuji et al. 1991; Martin 2011). This theory has obtained a high degree of credibility based upon palaeomagnetic studies (Otofuji et al. 1985). By the point at which the landmasses of the Proto-Japanese Islands had substantially formed, eastern and western Japan remained separated by a sea zone called the Fossa Magna, during the period around 15–5 Ma (Fig. 8.2c–e). In fact, many organisms have been strongly affected by these geohistorical conditions.

The separation process of the Japanese Archipelago from the Eurasian Continent (i.e., the formation of the Sea of Japan) was a result of crustal plate movements (i.e., plate tectonics). The crust of the earth is made up of ten or more major crustal plates. The Japanese Islands are located at the junction of four major tectonic plates—two continental plates (the Eurasian Plate and the North American Plate) and two oceanic plates (the Philippine Sea Plate and the Pacific Plate) (Fig. 8.2f; Seno et al. 1993). Geohistorically, the Japanese Islands were formed by means of subduction catatonics including accretionary catatonics, large-scale metamorphism, magmatism, and volcanism. Its geological structure is formed mainly of accretionary complex, metamorphic rocks, plutonic and volcanic rocks, and surface sediments.

As a result of this situation, the Japanese Islands have become an area highly prone to earthquakes, and the volcanic frontline runs the length of the Archipelago. Therefore, Japan is a region unique in the world, being constantly affected by drastic crustal deformation.

The diversity of insects in Japan is strongly influenced by (1) Palaeo-Japan having been located at the eastern margin of the Eurasian Continent; (2) the independent origin of northeastern and southwestern Japan, which greatly contributed to the establishment of insect diversity; (3) that subsequent to the formation of the Japanese Islands, a number of new lineages also arrived via land bridges during the Ice Ages and established populations; and (4) the wet and humid climate, and the climate diversity of each region, also contributed to the establishment of insect diversity. As described, the high degree of insect diversity of Japan has been established and supported, and is perpetuated, as a result of many complex factors aforementioned.

8.2 Molecular Phylogeography of Insects in Japan

From a biogeographic perspective, Japan is one of the most interesting regions in the world because of such complicated geohistorical formations. As such, many valuable phylogeographic studies of the Japanese Archipelago have been conducted.

In recent years, phylogeographic studies using molecular markers have been widely deployed. In particular, with regard to non-flying carabid beetles, such molecular phylogenetic studies have been undertaken for an extended period, from which a number of achievements have accumulated (Su et al. 1996a, b, 1998; Osawa et al. 1999; Sota and Vogler 2001; Sota et al. 2001; Sota 2002; Sota and Nagata 2008). In addition, molecular phylogeographic studies of other insects relatively popular in human society (i.e., butterflies, beetles) have also been conducted. Recently, a variety of insect taxa have been targeted for analyses by means of molecular phylogeographic studies.

In this section, we discuss several of such case studies conducted in the authors' laboratory that have focused on aquatic insects. Aquatic insects have an extremely important role in the studies of species diversity and phylogeography. They offer high potential to effectively investigate various evolutionary issues; that is, they are key taxa in typical biogeography and evolutionary biology.

8.2.1 Molecular Phylogeography of Aquatic Insects in Japan

The habitat of aquatic insects are limited to water areas. Especially, for aquatic insects, rivers are predominant habitats. Therefore, the potential for migration or dispersion of aquatic insects is strongly limited in a generally linear-type direction along the flow path of rivers, which is in contrast to terrestrial insects that can move in all directions. These strong constraints on dispersal potential are an important aspect facilitating productive investigations into their phylogeography.

Various aquatic insects are primarily adapted to lotic water environments (i.e., running water) such as the main river course, but are also partially adapted to lentic water environments such as pools, floodplains, swamps, and back marshes.

These river system networks are spatially structured in a hierarchical manner. The habitats of aquatic insects are connected in a linear structure with smaller streams progressively flowing into larger streams, and coming to form larger and larger networks (Bohonak and Jenkins 2003; Hughes 2007; Tojo 2010). These networks are composed of many patterns of habitat heterogeneity. Within the length of a river's linear network, habitats hierarchically and drastically change from the upstream to downstream areas (Campbell and McIntosh 2013; Miyazono and Taylor 2013). The physical attributes of the landscape influence the particular distributional pattern and population structure of species (Kindlmann and Burel 2008; Tojo 2010; Alp et al. 2012; Hughes et al. 2013). Through the transitions in the spatial layout of the landscape along a river system, hierarchies exist as follows: relative to the altitude of stream, the segment scale (e.g., headwater, upstream, midstream, downstream), the reach scale (e.g., one of the meandering sections, repetition of riffles and pools), and the microhabitat scale (e.g., changes in the substrate coarseness, water depth, sunshine condition, and their heterogeneity). These are all key factors determining the population and genetic structures of river organisms (Bohonak and Jenkins 2003; Hughes 2007). In addition, the geohistorical and environmental factors (water quality), and the biological and ecological factors (existence of other species) can also be important in determining resultant population and genetic structures of species. Additionally, the time scale of their life cycle and dispersal ability are also important determinants of their population and genetic structures (Hughes et al. 2009, 2013; Öckinger et al. 2010). Evaluating the relative role within and among streams in terms of the connectivity of populations (i.e., migration and dispersion potential) in a riverine landscape is crucial to developing a better understanding of stream ecology (Bohonak and Jenkins 2003; Wilcock et al. 2007; Krosch et al. 2011).

The ability to clearly distinguish the hierarchy as just described is a significant topic in the discussion of population structure and corresponding genetic structures, that is, with respect to molecular phylogeography. In addition, 109 comparatively large rivers in Japan have been targeted in the national research project, the National Censuses on River Environments being conducted by the Japanese Ministry of Land, Infrastructure, Transport and Tourism. In this project, it is highly important that the exhaustive distribution and population structure information of many aquatic insects has been gathered, and accumulated for more than 20 years. In this section, we discuss some case studies on such aquatic insects.

8.2.2 Deep Relationship of Genetic Structure with the Geohistory of Japan

8.2.2.1 Phylogeography of the Headwater-Specific Caddisfly, *Palaeagapetus* spp.

The eastern and western parts of Japan were independently separated by the sea embayment in the Fossa Magna region. With respect to the genetic structure of some aquatic insect groups, the geohistory of Japan has been engraved clearly within their genome. A typical example is the spring brook headwater-specific caddisflies (Trichoptera), of the genus *Palaeagapetus*. Caddisflies of this genus are typical specialists, being dependent upon mosses of a particular group, the Marchantiophyta, for food and habitat. These caddisflies live in a nest case formed from fragments of the leaves of this moss. They develop to become pupae among this moss's leaves; adults also live around this moss; and mated females lay their eggs on the leaves of the moss. That is, they depend completely upon this moss throughout their entire life cycle. In the dispersion of these caddisflies, the presence of this moss is obligatory. Then, their dispersion is considered to be severe. And as a result, it is an ideal species for phylogeographic studies.

Nine extant species of caddisflies of this genus have been described in the world. Seven of these species have been recorded in East Asia (the Japanese Archipelago, the Korean Peninsula, Sakhalin, and Russian Prymorye), and two in North America. Of these, six have been recorded within the Japanese Archipelago.

The relationships of all the nine species of *Palaeagapetus* caddisflies are shown in Fig. 8.3, on the basis of genetic analyses inferred from their nuclear DNA (histone H3 and CAD regions) and their mitochondrial DNA (COI and 16S rRNA regions). With regard to both analyses conducted on these genetic markers, these caddisflies are clearly shown to be composed of two major substantially genetically differentiated clades. We had expected that differentiation would be observed primarily between the Eurasian and North American Continental populations. However, the actual results were quite different. Furthermore, surprisingly, the geographic boundary between these two clades was clearly indicated as being in the center of the Japanese Islands (i.e., center of Honshu) (Fig. 8.3). This genetic boundary almost substantially corresponds to the westernmost side of Fossa Magna, the Itoigawa-Shizuoka Tectonic Line. Therefore, it is considered that this unique result conforms closely to the 'double-door' geohistorical model of the Japanese Archipelago, being almost consistent with the results of the estimated age of genetic differentiation.

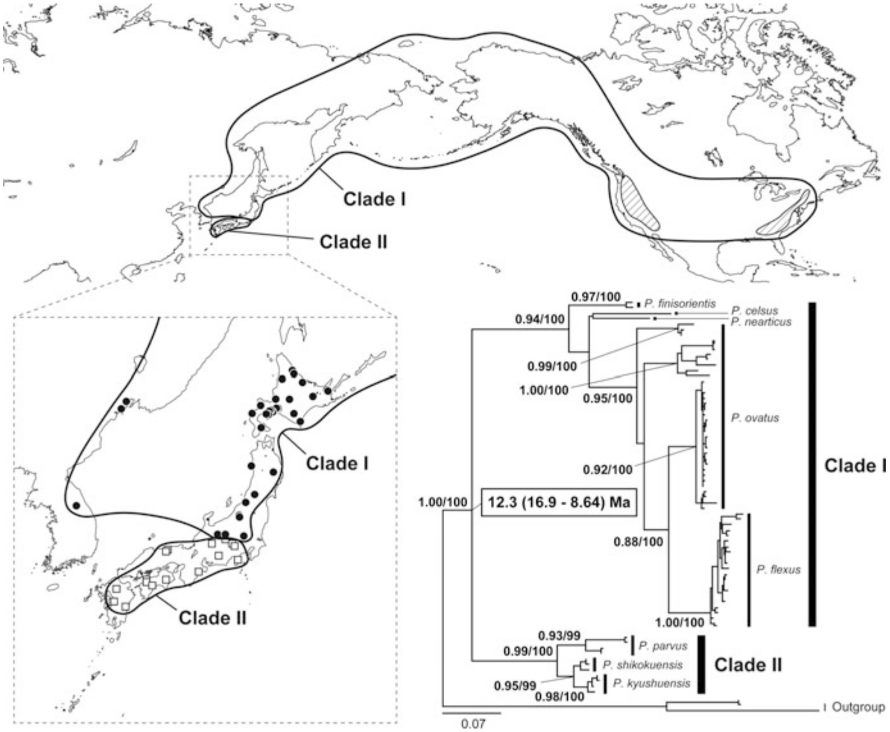


Fig. 8.3 Estimated Bayesian phylogeny of all species of *Palaeagaapetus* caddisflies based on a concatenated data set (1645 bp) of the mitochondrial DNA COI and 16S rRNA regions, and nuclear DNA histone H3 and CAD regions. *Numbers at major nodes* indicate the ML bootstrap support and the Bayesian posterior probabilities. *Numbers around each node* indicate the estimated divergence times, and represent 95 % credibility estimates for node ages. To estimate nodal divergence times of the genealogical lineages of *Palaeagaapetus* species, a relaxed Bayesian molecular clock analysis was performed with BEAST ver. 1.7.1 (Drummond et al. 2012). The proposed insect molecular clock (COI + 16S rRNA substitution rate = 2.39 % per million years; Papadopoulou et al. 2010) was adopted

8.2.2.2 Phylogeography of the Mayflies *Isonychia japonica* and *Ephoron shigae*

Isonychia japonica is a mayfly (Ephemeroptera) distributed widely across East Asia. Especially within the Japanese Islands and inhabiting a wide range of environments, including both upstream and downstream areas, even within the same river basin. Therefore, we term this mayfly a typical ‘habitat generalist’ species. Our previous study elucidated the fact that this mayfly is composed of two major clades that are significantly genetically differentiated: the Japanese Archipelago clade (clade I + II + III) and the continental clade (clade IV) (Saito and Tojo 2016a). They also considered that this genetic differentiation was directly and strongly influenced by the formation process of the Japanese Archipelago

(Otofuji et al. 1985; Ninomiya et al. 2014). Within the Japanese Archipelago clade, further hierarchical genetic differentiation occurred by means of habitat partitioning and geohistorical isolation events: thereby, clade III adapted to the upstream regions of river systems, whereas the other clade (clade I + II) is adapted to the lower regions. In addition, with respect to the downstream-adapted clade of this mayfly, it was shown that they are composed of two subclades (clades I and II) that are genetically differentiated in Japan; that is, they are genetically differentiated parapatrically between eastern and western Japan. The authors suggested that such differentiation and adaptation at the strain level and adaptation rates at the intraspecific level contributed to an increase in their distribution ranges and adaptation rates at the intraspecies level, thus clarifying why this species is able to be a "habitat generalist" (Saito and Tojo 2016a).

Figure 8.4 shows a mitochondrial tree based on COI and 16S rRNA regions, whereas a multilocus analysis (using histone H3, ITS-2, COI, and 16S rRNA regions) yielded the same topology (Saito and Tojo 2016a, b). Genetic differentiations between eastern and western Japan are clearly shown. By an exhaustive sampling

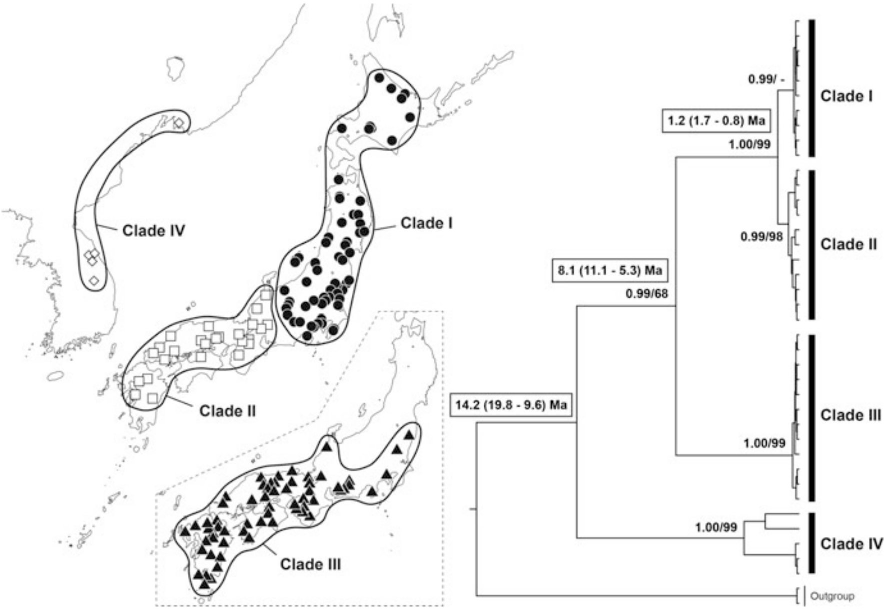


Fig. 8.4 Estimated Bayesian phylogenetic relationships of *Isonychia japonica* based on concatenated data of the mitochondrial DNA COI (573-bp) and 16S rRNA (375-bp) regions, and the distribution area of each clade. *Numbers at major nodes* indicate the maximum-likelihood (ML) bootstrap support, and the Bayesian posterior probabilities. *Number around each node* indicates the estimated divergence times, and represent 95 % credibility estimates for node ages. To estimate nodal divergence times of the genealogical lineages of this species, a relaxed Bayesian molecular clock analysis was performed with BEAST ver. 1.7.1 (Drummond et al. 2012). The proposed insect molecular clock (COI + 16S rRNA substitution rate = 2.39 % per million years; Papadopoulou et al. 2010) was adopted

from various regions across Japan, the genetic boundaries also substantially correspond to the westernmost side of Fossa Magna, the Itoigawa–Shizuoka Tectonic Line. However, the period in which divergence occurred for these clades is not comparatively deep in the past (i.e., 1.2 Ma); more recent geohistorical events (e.g., formation of the central mountain ranges, the Japan Alps; Sueoka et al. 2015; Saito and Tojo 2016a) are considered to be the origin of this divergence rather than the original formation of the Japanese Archipelago.

Similarly, for the mayfly *Ephoron shigae*, the presence of two major significantly differentiated clades in the Japanese Archipelago has also been revealed (Fig. 8.5) (Sekiné et al. 2013, 2015a, b, c). Here we show the results of the mitochondrial DNA (a combined tree of the COI and 16S rRNA regions) (Fig. 8.5); again, a multilocus analysis based on both nuclear (histone H3, EF-1α, ITS-2, and boule regions) and mitochondrial (COI and 16S rRNA regions) markers also showed the same tree topology (Sekiné et al., unpublished data).

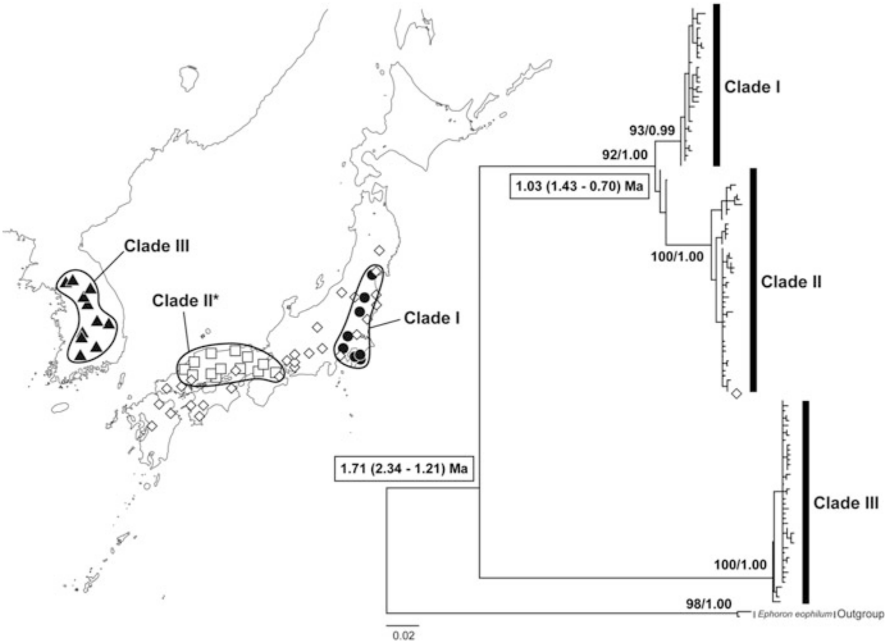


Fig. 8.5 Estimated Bayesian phylogenetic relationships of *Ephoron shigae* based on the mitochondrial DNA COI (636 bp) and 16S rRNA (373 bp). All specimens from unisexual populations across Japan were found to possess the same respective sequence types ◆ in each gene region. *Numbers at major nodes* indicate the ML bootstrap support and the Bayesian posterior probabilities. *Number around each node* indicates the estimated divergence times, and represent 95 % credibility estimates for node ages. To estimate nodal divergence times of the genealogical lineages of this species, a relaxed Bayesian molecular clock analysis was performed with BEAST ver. 1.7.1 (Drummond et al. 2012). The proposed insect molecular clock (COI + 16S rRNA substitution rate = 2.39 % per million years; Papadopoulou et al. 2010) was adopted

In this mayfly species, the populations of the Japanese Archipelago (i.e., clade I + II) and populations in the Korean Peninsula (i.e., clade III) have differentiated genetically, and this divergence age was estimated to be 1.71 Ma. This estimated divergence age is well consistent with the formation timing of the Tsushima Strait (1.55 Ma; Kitamura and Kimoto 2006; Osozawa et al. 2012). Thus, the existence of the Tsushima Strait must have significantly contributed to the biogeographic barrier among *E. shigae* populations.

8.2.2.3 Phylogeography of the Giant Water Bugs, *Appasus japonicus* and *Appasus major*

The giant water bugs *Appasus japonicus* and *Appasus major* are typical lentic water insects, inhabiting side pools and bights of rivers, relatively gentle stream portions, wetlands, and back marshes. In the Japanese Islands, many floodplains have been attenuated by artificial development, and so agricultural ponds and rice paddies have been used as their alternate habitats (Suzuki et al. 2013). However, in their alternate habitats, they also have been rapidly disappearing as the result of agricultural field maintenance and development. For these reasons, both species of these giant water bugs were recorded as being endangered species (Red List species) by the Ministry of the Environment of Japan and by some local governments. Because their dispersal ability is not so strong, they are one of the more suitable aquatic insect groups for phylogeographic studies.

As the results of genetic analyses inferred from the nuclear DNA (histone H3) and mitochondrial DNA (COI and 16S rRNA regions), extremely contrasting genetic structures have been identified between these closely related species, *A. japonicus* and *A. major* (Suzuki et al. 2014).

In *A. japonicus*, specimens from the Korean populations (clade III) constituted a single monophyletic clade and were a sister group of those in the western portion of the Japanese Archipelago (clade II). However, the Eastern Japanese clade (clade I) was clearly differentiated from the Western clade (Fig. 8.6).

On the other hand, four major clades were recognized within *A. major* (Fig. 8.7). Specimens from the Japanese and Korean populations revealed two distinct monophyletic clades. Significant differentiation was clearly observed between their genetic structures. Furthermore, the results of mismatch distribution and Bayesian skyline plot analyses suggested the possibility of a bottleneck effect or founder effect within two of the *A. major* clades (Suzuki et al. 2014). Collectively, these results demonstrated both similarities and differences between these two species even though their distributions widely overlap in East Asia, with their morphological characteristics and ecological niches being very similar. These differences in genetic structures are considered to be caused by their evolutionary history. In particular, clade II of *A. japonicus* (Kyushu and Chugoku regions) and the Korean clade III, together constituted a single monophyletic clade, so the Japanese *A. japonicus* (clade I + II) was evaluated as being paraphyletic in relationship to the continental *A. japonicus* (Fig. 8.6). Thus, the possibility of redispersion (i.e.,

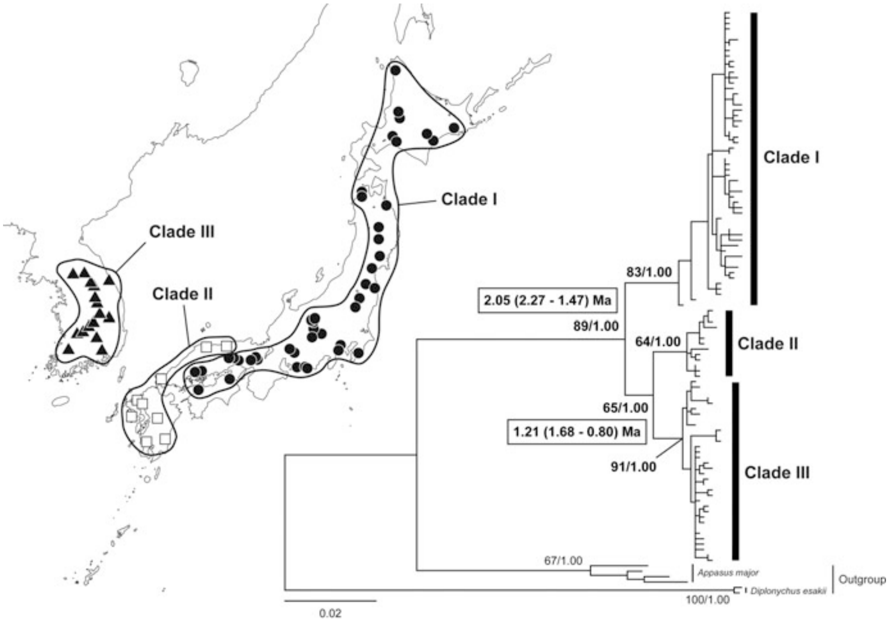


Fig. 8.6 Estimated Bayesian phylogenetic relationships of *Appasus japonicus* based on concatenated data (1093 bp) of the mitochondrial DNA COI and 16S rRNA regions and the distribution area of each clade of *Appasus japonicus*. *Numbers at major nodes* indicate the ML bootstrap support and the Bayesian posterior probabilities. *Number around each node* indicates the estimated divergence times, and represent 95 % credibility estimates for node ages. To estimate nodal divergence times of the genealogical lineages of this species, a relaxed Bayesian molecular clock analysis was performed with BEAST ver. 1.7.1 (Drummond et al. 2012). The proposed insect molecular clock (COI + 16S rRNA substitution rate = 2.39 % per million years; Papadopoulou et al. 2010) was adopted

'back dispersion') has been strongly suggested from the Japanese Islands (Kyushu and Chugoku populations) to the Eurasian Continent (the Korean Peninsula) (Suzuki et al. 2014).

In *A. major*, major clades within the Japanese Archipelago were clearly differentiated by mountain ranges, that is, the Ou mountain range and central mountainous region. Because their differentiation ages as estimated (i.e., between clade I and II, and between the clades I, II, and III) substantially coincide with the geologically understood timing of mountain formation (mountain-building activity), it is considered to be a typical example of genetic differentiation (Fig. 8.7) (Suzuki et al. 2014).

In these two species, *A. japonicas* and *A. major*, genetic differentiation between the Japanese and continental clades was also strongly attributed to the formation of the Tsushima Strait (estimated divergence age: 1.21 Ma in *A. japonicus*, 1.53 Ma in *A. major*). In addition, the estimated divergence age of *A. major* was slightly earlier than that of *A. japonicus* (Figs. 8.6, 8.7). These slight genetic differences between

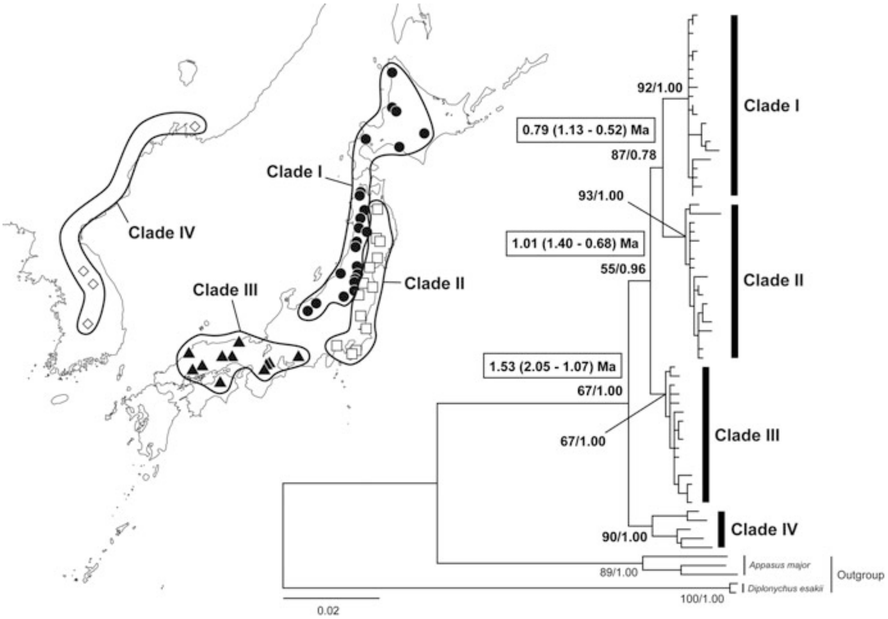


Fig. 8.7 Estimated Bayesian phylogeny of *Appasus major* based on concatenated data (1093 bp) of the mitochondrial DNA COI and 16S rRNA regions and the distribution area of each clade of *Appasus major*. *Numbers at major nodes* indicate the ML bootstrap support, and the Bayesian posterior probabilities. *Number around each node* indicates the estimated divergence times, and represent 95 % credibility estimates for node ages. To estimate nodal divergence times of the genealogical lineages of this species, a relaxed Bayesian molecular clock analysis was performed with BEAST ver. 1.7.1 (Drummond et al. 2012). The proposed insect molecular clock (16S rRNA substitution rate = 2.39 % per million years; Papadopoulou et al. 2010) was adopted

populations across the Tsushima Strait may be related to the difference in their ability to disperse.

8.2.2.4 Phylogeography of the Headwater-Specific Mayfly *Dipteromimus tipuliformis*

Dipteromimidae is a family endemic to Japan. As such, being endemic to Japan at the family level is an extremely rare circumstance (Tojo and Matsukawa 2003; Takenaka et al. 2015). The validity of the systematic positioning of Dipteromimidae at the family level has not yet been clearly established. The mayfly order Ephemeroptera is one of the most basal clades of winged insects, Pterygota. Since ancestral groups of mayflies originated approximately 400 Ma (Engel and Grimaldi 2004), it is extremely difficult to clarify such systematic relationships at the higher taxon level. The family Dipteromimidae consists of only two species of the genus *Dipteromimus* (Fig. 8.8). Of these, *Dipteromimus tipuliformis* is

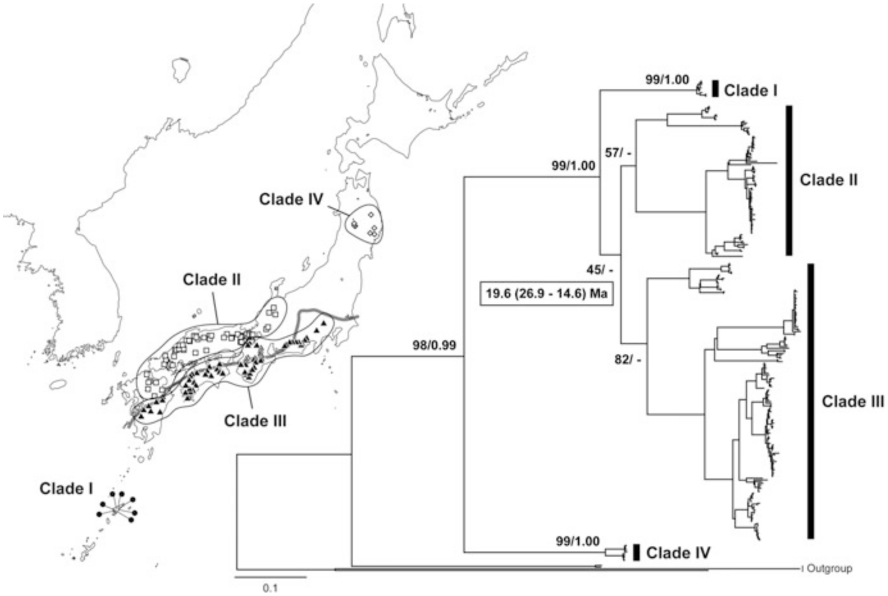


Fig. 8.8 Estimated ML phylogeny of *Dipteromimus tipuliformis* based on mitochondrial 16S rRNA region (1166 bp) and the distribution area of each clade of their local population. *Numbers at major nodes* indicate the ML bootstrap support, and the Bayesian posterior probabilities. *Number around each node* indicates the estimated divergence times, and represent 95 % credibility estimates for node ages. To estimate nodal divergence times of the genealogical lineages of this species, a relaxed Bayesian molecular clock analysis was performed with BEAST ver. 1.7.1 (Drummond et al. 2012). The proposed insect molecular clock (COI + 16S rRNA substitution rate = 2.39 % per million years; Papadopoulou et al. 2010) was adopted

distributed widely throughout southwestern Honshu, Shikoku, and in the Kyushu Islands, including Amami-oshima Island. The other species *Dipteromimus flavipterus* inhabits only the Tohoku region of Honshu (Tojo and Matsukawa 2003; Takenaka et al. 2015). It is extremely interesting that the former species is distributed even on Amami-oshima Island, beyond the Tokara Gap, that is, in both the Palearctic and Oriental Regions. Because these mayflies inhabit such a special habitat (i.e., small pools or side pools of brooks) of the headwater environment, and their dispersal ability is extremely weak, it is known that an extremely large degree of genetic differentiation exists at the local population level (Fig. 8.8) (Tojo and Matsukawa 2003; Tojo 2005, 2010). Their significant level of genetic differentiation between relatively nearby populations has been previously reported.

The results of their phylogeographic analyses inferred from the nuclear DNA (histone H3, 28S rRNA regions) and the mitochondrial DNA (COI and 16S rRNA regions) show several interesting features. Both species of this family exhibit a large degree of genetic differentiation, and that differentiation is considered to have occurred in an extremely ancient time period (Fig. 8.8). In the analysis of the mitochondrial DNA COI region, which is frequently used for the DNA barcoding method, it was observed that the degree of nucleotide substitution was extremely large, and it had reached saturation level. As a result, the analyses of the 16S rRNA, histone H3, and 28S rRNA regions (which are often used for higher-level phylogenetic analyses) were effective.

Initially, in *D. tipuliformis*, a large degree of observed genetic differentiation was found to be bounded by the Tokara Gap between Amami-oshima and Kyushu Islands. However, the populations of Honshu, Shikoku, and Kyushu were genetically differentiated by an extremely specific boundary line extending in an east–west direction across these three islands, rather than the differentiation being observed among these three islands. More interestingly, this genetic boundary was shown to correspond to the Median Tectonic Line (MTL), which is the largest fault of Japan (Fig. 8.8). This genetic differentiation across the MTL is also supported strongly by ANOVA analysis. Although the geological origin of the MTL was about 130 Ma (Taira 1990, 2001; Taira et al. 1997), the active period is considered to be about 20 Ma (Yanai et al. 2010). As such, the geohistory corresponds admirably well with the results of the estimated differentiation age (i.e., between the regions to the north and south of the MTL), which was 19.6 Ma based on the molecular clock.

8.3 Conclusions

In this chapter, we reviewed the actual status of species diversity of insects in Japan, and also discuss the factors contributing to their diversity. In addition, we introduced examples of genetic differentiation and species differentiation that are deeply associated with the geohistory of Japan, especially focusing on aquatic insects.

In the *Palaeagapetus* caddisflies, surprisingly, a boundary between the world's two major clades was identified to be present within the Japanese Archipelago. The mayflies *Isonychia japonica* and *Ephoron shigae* have been shown to be genetically differentiated across the Tsushima Strait, and also between eastern and western Japan. In particular within the species *I. japonica*, the genetic differentiation and observable ecological niche differentiation is very clear. In addition, contrasting genetic structures of the closely related giant water bugs *Appasus japonicas* and *Appasus major* were also clearly observed, which were considered to be the result of their different evolutionary history. Furthermore, in *A. japonicus* the 'back dispersal' phenomenon is considered to be highly probable; that is, the distribution of this species re-dispersed back to the continent from the Japanese Archipelago. Finally, within the mayfly species, *Dipteromimus tipuliformis*, being a family endemic to Japan, an extremely large degree of genetic differentiation at the regional population level was clearly observed. Therein, it became clear that their genetic differentiation also reflects the geological history of Japan very well.

As such, one after another, many cases of geohistorical boundaries along tectonic lines resulting in genetic differentiation have been identified. Generally, Japan has been thought as being just a small chain of islands having many natural disasters, that is, many earthquakes and volcanic activity. However, we think of these islands as a place with extremely high potential to foster biodiversity, in particular among its freshwater insects, as shown in a variety of studies of phylogeography and evolutionary biology.

Finally, molecular phylogeographic studies of aquatic insects in Japan have gotten underway. However, as noted in this chapter, aquatic insects are very well suited as species for discussion on biogeography, and the potential for outcomes that provide clear and useful results is considered to be very high. Before these recently initiated studies, some interesting research findings have accumulated in regard to various Japanese freshwater fish and amphibian species. In the future, by focusing on freshwater insects, which are comparatively more ancestral, the development of productive discussion in the context of the geohistory of more ancient ages, such as the initial formation stages of the Japanese Archipelago, is expected.

References

Alp M, Keller I, Westram AM, Robinson CT (2012) How river structure and biological traits influence gene flow: a population genetic study of two stream invertebrates with differing dispersal abilities. Freshw Biol 57:969–981

Barnes GL (2003) Origins of the Japanese Islands: the new “big picture”. Jpn Rev 15:3–50

Bohonak AJ, Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol Lett 6:783–796

Campbell RE, McIntosh AR (2013) Do isolation and local habitat jointly limit the structure of stream invertebrate assemblages? Freshw Biol 58:128–141

Cardé RT, Resh VH (2012) A world of insects. Harvard University Press, Cambridge, MA. 404 pp

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol Biol Evol 29:1969–1973

Engel MS, Grimaldi DA (2004) New light shed on the oldest insect. Nature (Lond) 427:627–630

Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, New York, 755 pp

Gullan PJ, Cranston PS (2010) The insects: an outline of entomology. Wiley, Oxford. 565 pp

Hayashida A, Fukui A, Torii M (1991) Paleomagnetism of the early Miocene Kani Group in Southwest Japan and its implication for the opening of the Japan Sea. Geophys Res Lett 18: 1095–1098

Hirashima Y, Morimoto K, Tadauchi O (1989) Taxonomy of insects (Konchu Bunrui-gaku). Kawashima Shoten, Tokyo. 597 pp (in Japanese)

Hughes JM (2007) Constraints on recovery: using molecular methods to study connectivity of aquatic biota in rivers and streams. Freshw Biol 52:616–631

Hughes JM, Schmidt DJ, Finn DS (2009) Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. Bioscience 59:573–583

Hughes JM, Huey JA, Schmidt DJ (2013) Is realised connectivity among populations of aquatic fauna predictable from potential connectivity? Freshw Biol 58:951–966

Kindlmann P, Burel F (2008) Connectivity measures: a review. Landsc Ecol 23:879–890

Kitamura A, Kimoto K (2006) History of the inflow of the warm Tsushima current into the sea of Japan between 3.5 and 0.8 Ma. Palaeogeogr Palaeoclimatol Palaeoecol 236:355–366

Krosch MN, Baker AM, Mather PB, Cranston PS (2011) Spatial population genetic structure reveals strong natal site fidelity in *Echinocladius martini* (Diptera: Chironomidae) in Northeast Queensland, Australia. Freshw Biol 56:1328–1341

Martin AK (2011) Double saloon door tectonics in the Japan Sea, Fossa Magna, and the Japanese Island Arc. Tectonophysics 498:45–65

Misof B, Liu S, Meusemann K, Peters RS et al (2014) Phylogenomics resolves the timing and pattern of insect evolution. Science 346:763–767

Miyazono S, Taylor CM (2013) Effects of habitat size and isolation on species immigration–extinction dynamics and community nestedness in a desert river system. Freshw Biol 58: 1303–1312

Ninomiya T, Shimoyama S, Watanabe K, Horie K, Dunkley DJ, Shiraishi K (2014) Age of the Taishu Group, Southwestern Japan, and implications for the origin and evolution of the Japan Sea. Island Arc 3:206–220

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS, Bommarco R (2010) Life-history traits predict species responses to habitat area and isolation: a cross continental synthesis. Ecol Lett 13:969–979

Osawa S, Su Z-H, Kim C, Okamoto M, Tominaga O, Imura Y (1999) Evolution of the carabid ground beetles. Adv Biophys 36:65–106

Osozawa S, Shinjo R, Armid A, Watanabe Y, Horiguchi T, Wakabayashi J (2012) Palaeogeographic reconstruction of the 1.55 Ma synchronous isolation of the Ryukyu Islands, Japan, and Taiwan and inflow of the Kuroshio warm current. Int Geol Rev 54:1369–1388

Otofuji Y, Matsuda T, Nohda S (1985) Opening mode of the Japan Sea inferred from paleomagnetism of the Japan Arc. Nature (Lond) 317:603–604

Otofuji Y, Itaya T, Matsuda T (1991) Rapid rotation of Southwest Japan–paleomagnetism and K-Ar ages of Miocene volcanic rocks of southwest Japan. Geophys J Int 105:397–405

Ozono A, Kawashima I, Futahashi R (2012) Dragonflies of Japan (Nihon no Tombo). Bun-ichi, Tokyo, 532 pp (in Japanese)

Papadopoulou A, Anastasiou I, Vogler AP (2010) Revisiting the insect mitochondrial molecular clock: the Mid-Aegean trench calibration. Mol Biol Evol 27:1659–1672

Saito R, Tojo K (2016a) Complex geographic and habitat-based niche partitioning of an East Asian habitat generalist mayfly *Isonychia japonica* (Ephemeroptera, Isonychiidae), with reference to differences in genetic structure. Freshw Sci 35:712–723

Saito R, Tojo K (2016b) Comparing spatial patterns of population density, biomass, and genetic diversity patterns of the habitat generalist mayfly *Isonychia japonica* Ulmer (Ephemeroptera, Isonychiidae), in the riverine landscape of the Chikuma-Shinano River Basin. Freshw Sci 35:724–737

Schoville SD, Uchifune T, Machida R (2013) Colliding fragment islands transport independent lineages of endemic rock-crawlers (Grylloblattodea: Grylloblattidae) in the Japanese Archipelago. Mol Phylogenet Evol 66:915–927

Sekiné K, Hayashi F, Tojo K (2013) Phylogeography of the East Asian polymitarcyid mayfly genus *Ephoron* (Ephemeroptera Polymitarcyidae): a comparative analysis of molecular and ecological characteristics. Biol J Linn Soc 109:181–202

Sekiné K, Tojo K, Bae YJ (2015a) Distribution and genetic characteristics of *Ephoron shigae* (Ephemeroptera: Polymitarcyidae) in Korea. Entomol Res 45:150–157

Sekiné K, Tojo K, Bae YJ (2015b) Facultative parthenogenesis in the burrowing mayfly *Ephoron eophilum* (Ephemeroptera: Polymitarcyidae) with an extremely short alate stage. Eur J Entomol 112:606–612

Sekiné K, Hayashi F, Tojo K (2015c) Unexpected monophyletic origin of Ephoron shigae unisexual reproduction strains and their rapid expansion across Japan. R Soc Open Sci 2:150072

Seno T, Stein S, Gripp AE (1993) A model for the motion of the Philippine Sea plate consistent with NUVEL-1 and geological data. J Geophys Res 98:17941–17948

Sota T (2002) Radiation and reticulation: extensive introgressive hybridization in the carabid beetles *Ohomopterus* inferred from mitochondrial gene genealogy. Popul Ecol 44:145–156

Sota T, Nagata N (2008) Diversification in a fluctuating island setting: rapid radiation of *Ohomopterus* ground beetles in the Japanese Islands. Philos Trans R Soc Lond 363:3377–3390

Sota T, Vogler AP (2001) Incongruence of mitochondrial and nuclear gene trees in the carabid beetles *Ohomopterus*. Syst Biol 50:39–59

Sota T, Ishikawa R, Ujiie M, Kusumoto F, Vogler A (2001) Extensive trans-species mitochondrial polymorphisms in the carabid beetles *Carabus* subgenus *Ohomopterus* caused by repeated introgressive hybridization. Mol Ecol 10:2833–2847

Su Z-H, Ohama T, Okada TS, Nakamura K, Ishikawa R, Osawa S (1996a) Geography-linked phylogeny of the *Damaster* ground beetles inferred from mitochondrial ND5 gene sequences. J Mol Evol 42:130–134

Su Z-H, Tominaga O, Ohama T, Kajiwara E, Ishikawa R, Okada TS, Nakamura K, Osawa S (1996b) Parallel evolution in radiation of *Ohomopterus* ground beetles inferred from mitochondrial ND5 gene sequences. J Mol Evol 43:662–671

Su ZH, Tominaga O, Okamoto M, Osawa S (1998) Origin and diversification of hindwingless *Damaster* ground beetles within the Japanese islands as deduced from mitochondrial ND5 gene sequences (Coleoptera, Carabidae). Mol Biol Evol 15:1026–1039

Sueoka S, Tsutsumi H, Tagami T (2015) Development of low-temperature thermochronology and its application to uplift and denudational history of Japanese mountains. Earth Sci 69:47–70 (in Japanese)

Suzuki T, Tanizawa T, Sekiné K, Kunimi J, Tojo K (2013) Morphological and genetic relationship of two closely-related giant water bugs: *Appasus japonicus* Vuillefroy and *Appasus major* Esaki (Heteroptera: Belostomatidae). Biol J Linn Soc 110:615–643

Suzuki T, Kitano T, Tojo K (2014) Contrasting genetic structure of closely related giant water bugs: phylogeography of *Appasus japonicus* and *Appasus major* (Insecta: Heteroptera, Belostomatidae). Mol Phylogenet Evol 72:7–16

Taira A (1990) The origin of the Japanese Island Arc (Nihon Retto no Tanjo). Iwanami Shoten, Tokyo, 226 pp (in Japanese)

Taira A (2001) Tectonic evolution of the Japanese Island arc system. Annu Rev Earth Planet Sci 29:109–134

Taira A, Kiyokawa S, Aokike K, Saito S (1997) Accretion tectonics of Japanese Islands and evolution of continental crust. Earth Planet Sci 325:467–478

Takenaka M, Kogawara H, Tojo K (2015) The distribution range of the dipteromimid mayflies (Ephemeroptera, Dipteromimidae). New Entomol 64:13–18 (in Japanese with English abstract)

Tojo K (2005) Genetic diversity in a headwater-specific aquatic insect *Dipteromimus tipuliformis* McLachlan (Ephemeroptera, Dipteromimidae), based on the mitochondrial 16S rRNA gene sequences. Ecol Civil Eng Soc 7:119–127 (in Japanese with English abstract)

Tojo K (2010) The current distribution of aquatic insects inhabiting river systems, with respect to their population and genetic structure. In: Harris EL, Davies NE (eds) Insect habitats: characteristics, diversity and management. Nova Science, New York, pp 157–161

Tojo K, Matsukawa K (2003) A description of the second species of the family Dipteromimidae (Insecta, Ephemeroptera), and genetic relationship of two dipteromimid mayflies inferred from mitochondrial 16S rRNA gene sequences. Zool Sci 20:1249–1259

Uchifune T, Machida R (2005) Grylloblattodea: a proposed affinity between Grylloblattodea and Mantophasmatodea. Biol Sci (Tokyo) 57:35–39 (in Japanese)

Wilcock HR, Bruford MW, Nichols RA, Hildrew AG (2007) Landscape, habitat characteristics and the genetic population structure of two caddisflies. Freshw Biol 52:1907–1929

Yanai S, Aoki K, Akahori Y (2010) Opening of Japan Sea and major tectonic lines of Japan: MTL, TTL and Fossa Magna. J Geogr 119:1079–1124

Chapter 9
Species Diversity and Phylogeny of Freshwater and Terrestrial Gammaridean Amphipods (Crustacea) in Japan

Ko Tomikawa

Abstract Gammaridea (Amphipoda) comprises approximately 7900 species. To date, 37 freshwater species from 8 families and 21 terrestrial species from 1 family have been recorded in Japan. The Japanese freshwater amphipod fauna is characterized by high endemism at the species level. Among the 36 native species, 32 (~89 %) are endemic. However, at the family level, endemism is quite low, and commonality with China, Russia, and North America is high. It is generally accepted that freshwater amphipods evolved from marine ancestors. As inferred from molecular data, amphipods have repeatedly switched between marine and freshwater habitats during their evolutionary history. Similarly, invasions of groundwater habitats have occurred independently in different lineages. In general, troglobitic amphipods are characterized by either the loss or rudimentation of eyes and pigment, attenuation of the body or appendages, and development of surface setae. These morphological features are probably an adaptation to life in subterranean environments. Talitridae is the only amphipod group that invades terrestrial environments. The following six types of distribution are recognized: (1) widely distributed from Hokkaido to Okinawa across the Tsugaru and Tokara Straits; (2) distributed south of the Tsugaru Strait (across the Tokara Strait); (3) distributed between south of the Tsugaru Strait and north of the Tokara Strait; (4) distributed north of the Tokara Strait (across the Tsugaru Strait); (5) distributed north of the Tsugaru Strait; and (6) species in restricted distributional ranges.

Keywords Gammaridea • Amphipoda • Crustacea • Invasive • Range expansion • Phylogeny • Gammarid taxonomy

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9.1 Introduction

Amphipod crustaceans constitute a conspicuous and important component of many marine, freshwater, and terrestrial ecosystems. They comprise one of the most diverse crustacean groups, and more than 9600 species have been described (Horton et al. 2015); however, this number is expected to reach 25,000 when undescribed species are included (Bousfield 1978). Most species occur in the sea, from shallow to deep waters. Members of the Lysianassoidea are found in deep-sea thermal vents (Barnard and Ingram 1990). Some amphipods inhabit brackish and freshwater habitats, and others have even adapted to life in matter stranded on the seashore, in forest litter, and in hypogean waters. Approximately 1900 species have been recorded from inland freshwaters, which accounts for almost 20 % of total amphipod diversity (Horton et al. 2015).

Morphologically, amphipods share the following characteristics with other peracarids (e.g., isopods, mysids, cumaceans): the first thoracic segment is fused to the head; the eggs are borne in a brood pouch formed by oostegites (epipodites), and hatch into juveniles without a planktonic larval period; the mandible has a characteristic articulated projection called the *lacinia mobilis* between the molar and incisor processes. Peracarida is most closely related to Lophogastrida and Spelaeogriphacea, according to recent molecular analyses (Spears et al. 2005; Meland and Willassen 2007). Amphipods can be distinguished from other peracarids by the following combination of characters: laterally compressed body with coxae developed into plates; sessile eyes; seven pairs of uniramous pereopods (legs); absence of a carapace; and the absence of antennal squame (Fig. 9.1). Amphipods are unique among the peracarids in having coxal gills on pereopod coxae (the basal article); the anterior four pairs of pereopods point forward and the posterior three pairs backward; the abdomen has three pairs of multi-articulated swimming legs called pleopods and a few articulated legs called uropods (Fig. 9.1). Sexually mature individuals range from 1 to 340 mm in length.

Traditionally, Amphipoda has been divided into four suborders: Gammaridea, Caprellidea, Hyperiidea, and Ingolfiellidea. Gammaridea comprises approximately 7900 species; almost all the freshwater and terrestrial amphipods belong to this taxon. Several authors have proposed new amphipod classifications at the suborder level (Myers and Lowry 2003; Lowry and Myers 2013). Myers and Lowry (2003) elevated the gammaridean superfamily Corophioidea to the suborder Corophiidea, placing the previous suborder Caprellidea within it as the infraorder Caprellida. Senticaudata is a new suborder created by Lowry and Myers (2013), which they split off from Gammaridea. The former Caprellidea was put into Senticaudata as the superfamily Caprelloidea under the infraorder Corophiida. Senticaudata contains approximately 5000 species, which is more than half of the amphipod species described. However, this new classification is not widely accepted, because it was not based on firm phylogenetic analyses. In this chapter, the traditional suborder classification is adopted.

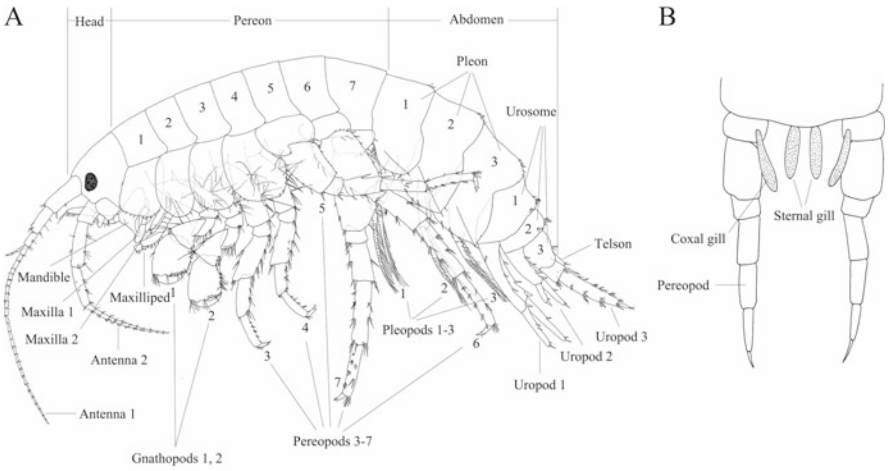

Fig. 9.1 External morphology of Amphipoda. (**a**) Habitus, lateral view. (**b**) Pereonite and pereopod, sagittal view. (Modified from Tomikawa and Morino 2012)

9.2 History of Gammaridean Amphipod Taxonomic Studies in Japan

The first taxonomic study of Japanese gammaridean amphipods was that of Martens (1868), who described the terrestrial *Orchestia humicola* (now *Platorchestia humicola*) from Yokohama. Marine gammaridean amphipods in Japan were recorded by Stebbing (1888), Stephensen (1932, 1933, 1938, 1944), Bulycheva (1936), and Dahl (1944). Akatsuka and Komai (1922) described three new subterranean species, *Pseudocrangonyx shikokunis*, *P. kyotonis*, and *P. yezonis*; these represent the first Japanese gammaridean amphipods described by Japanese authors. In the same year, Tattersal (1922) described two new freshwater amphipods, *Atyloides japonica* (now in *Sternomoera*) and *Gammarus annandalei* (now in *Jesogammarus*), and one new terrestrial species *Talorchestia japonica* (now in *Platorchestia*) from Lake Biwa and its adjacent areas.

Uéno (1927, 1971) significantly extended our knowledge of the freshwater and subterranean fauna by describing many new species and subspecies. The most notable of those is *Gammarus nipponensis* Uéno, 1940, which is widely distributed in western Japan and is abundant in freshwater environments.

Iwasa (1939), the first study on marine taxa by a Japanese taxonomist, reported 15 talitrid species including 2 terrestrial ones. Twenty years after Iwasa's report, a comprehensive study was conducted by Nagata (1965a, b, c) in the Seto Inland Sea. Among the 85 gammaridean amphipod species studied in his work, 21 were new to science. Hirayama (1983, 1988) carried out important studies on shallow-water amphipods, in which he investigated the western Kyushu fauna, recording

132 species and describing 62 new species. The number of known Japanese amphipods increased drastically as a result of Hirayama's studies.

Since the 1980s, a number of taxonomic works have been published: marine benthic taxa such as Aoridae (Ariyama 1996, 2004), Hyalidae (Hiwatari and Kajiwara 1981a, b; Hiwatari 2003), Melitidae (Yamato 1990), and Pleustidae (Ishimaru 1984); commensal taxa such as Colomastigidae (Ariyama 2005) and Leucothoidae (White and Reimer 2012); deep-sea taxa such as Lepechinellidae (Gamô 1981); freshwater taxa such as Anisogammaridae (Morino 1985; Tomikawa et al. 2006) and Gammaridae (Tomikawa et al. 2014b); subterranean taxa such as Luciobliviidae (Tomikawa et al. 2007b), Mesogammaridae (Tomikawa et al. 2007b), and Pontogeneiidae (Kuribayashi et al. 1996; Tomikawa et al. 2014a); and the terrestrial Talitridae (Morino and Miyamoto 2015).

Approximately 400 species of gammaridean amphipods have been recorded from Japan, including approximately 340 marine, 37 freshwater, and 21 terrestrial species. However, further taxonomic study is required, with many non-investigated areas still remaining in Japan. Species that are either newly recorded in Japan or new to science are published every year; it has been calculated that the number of identified gammaridean amphipod species will reach 1000 (Ishimaru 2001).

9.3 Diversity of Freshwater and Terrestrial Gammaridean Amphipods in Japan

Almost 1900 species of gammaridean amphipods are known from fresh- and inland waters worldwide. In Japan, 37 species, including 1 alien species, in 8 families have been recorded from freshwater environments (Table 9.1). Looking at the breakdown of native species habitats, there are 13 groundwater, 14 mountain stream and/or spring brook, and 9 lowland river- and/or lake-dwelling species, indicating that the diversity is relatively high in low temperature waters where few changes occur, particularly in groundwater. The Japanese freshwater amphipod fauna is characterized by high endemism at the species level. Among the 36 native species, 32 (~89 %) are endemic to Japan. However, at the family level, endemism is quite low, and commonality with China, Russia, and North America is observed; only Luciobliviidae is endemic to Japan.

Terrestrial gammaridean amphipods belong exclusively to Talitridae, which are distributed worldwide. To date, about 250 species have been described globally (Serejo and Lowry 2008). In Japan, 21 species in 13 genera have been recorded, including 1 undescribed species. Five genera, *Ezotinorchestia*, *Kokuborchestia*, *Minamitalitrus*, *Mizuhorchestia*, and *Nipponorchestia*, are endemic to Japan (Table 9.1).

Anisogammarid amphipods occur in littoral marine, intertidal, estuarine, and freshwater environments in the North Pacific Rim, but troglobitic species do not. This family is morphologically well defined, and its monophyly is strongly supported by molecular data (Tomikawa et al. 2010). In Japan, two genera,

Table 9.1 Species, distribution, and habitat of freshwater and terrestrial gammaridean amphipods in Japan

Species	Distribution in Japan	Habitat
Anisogammaridae		
Eogammarus kygi (Dershavin, 1923)	Hokkaido, northern Honshu	River, lake
Eogammarus itotomikoae Tomikawa, Morino, Toft and Mawatari 2006	Hokkaido	River
Jesogammarus annandalei (Tattersall, 1922)	Lake Biwa	Lake
Jesogammarus fluvialis Morino, 1985	Tokai, Kinki districts	Spring brook
Jesogammarus fujinoi Tomikawa and Morino, 2003	Northern Honshu	Spring brook
Jesogammarus hokurikuensis Morino, 1985	Northern Honshu	Spring brook
Jesogammarus ikiensis Tomikawa, 2015	Iki Isl.	River
Jesogammarus jesoensis (Schellenberg, 1937)	Hokkaido, northern Honshu	River, lake, spring brook
Jesogammarus mikadoi Tomikawa, Morino and Mawatari, 2003	Northern Honshu	Spring brook
Jesogammarus naritai Morino, 1985	Lake Biwa	Lake
Jesogammarus paucisetulosus Morino, 1984	Kanto district	Mountain stream
Jesogammarus shonaiensis Tomikawa and Morino, 2003	Northern Honshu	Spring brook
Jesogammarus spinopalpus Morino, 1985	Kanto district	River, lake
Jesogammarus suwaensis Morino, 1986	Lake Suwa, Lake Kawaguchi	Lake
Crangonyctidae		
Crangonyx floridanus Bousfield, 1963	Throughout Japan	River, lake
Gammaridae		
Gammarus koreanus Uéno, 1940	Goto Isl.	River
Gammarus mukudai Tomikawa, Soh, Kobayashi and Yamaguchi, 2014	Iki Isl., Tsushima Isl.	River
Gammarus nipponensis Uéno, 1940	Western Honshu, Shikoku, Kyushu	River
Kamakidae		
Kamaka biwae Uéno, 1943	Lake Biwa	Lake
Kamaka kuthae Dershavin, 1923	Hokkaido	River, lake
Kamaka morinoi Ariyama, 2007	Tohoku to Chugoku districts	River, lake
Luciobliviidae		
Lucioblivio kozaensis Tomikawa, 2007	Tokai, Kinki districts	Groundwater
Mesogammaridae		
Eoniphargus kojimai Uéno, 1955	Kanto, Tokai districts	Groundwater
Octopupilla felix Tomikawa, 2007	Kinki district, Shikoku	Groundwater

(continued)

Table 9.1 (continued)

Species	Distribution in Japan	Habitat
Pontogeneiidae		
Awacaris kawasawai Uéno,1971	Shikoku	Groundwater
Relictomoera relicta (Uéno, 1971)	Fukue Isl.	Groundwater
Steromoera japonica (Tattersall, 1922)	Eastern Honshu	Mountain stream
Sternomoera morinoi Tomikawa and Ishimaru, 2014	Kinki district	Groundwater
Sternomoera rhyaca Kuribayashi, Ishimaru and Mawatari, 1996	Hokkaido, Honshu	Coastal stream
Sternomoera tsushimana (Uéno, 1971)	Tsushima Isl.	Groundwater
Sternomoera yezoensis (Uéno, 1933)	Hokkaido	Spring brook
Pseudocrangonyctidae		
Eocrangonyx japonicus (Uéno, 1930)	Kanto district	Groundwater
Pseudocrangonyx asiaticus Uéno, 1934	Tsushima Isl.	Groundwater
Pseudocrangonyx coreanus Uéno, 1966	Chugoku district, Tsushima Isl.	Groundwater
Pseudocrangonyx kyotonis Akatsuka and Komai, 1922	Tokai, Kinki , Chugoku districts	Groundwater
Pseudocrangonyx shikokunis Akatsuka and Komai, 1922	Chugoku district, Shikoku	Groundwater
Pseudocrangonyx yezonis Akatsuka and Komai, 1922	Hokkaido, northern Honshu	Groundwater
Talitridae		
Bousfieldia omoto Morino, 2014	Ishigaki, Iriomote Isl.	Inland leaf litter
Ditmorchestia ditmari (Derzhavin, 1923)	Eastern Hokkaido	Littoral leaf litter
Kokuborchestia kokuboi (Uéno, 1929)	Southern Hokkaido to northern Honshu	Littoral to inland leaf litter
Minamitalitrus zoltani White, Lowry and Morino, 2013	Minamidaito Isl.	Cave
Mizuhorchestia urospina Morino, 2014	Honshu, Shikoku, Kyushu	Littoral to inland leaf litter
Nipponorchestia curvatus Morino and Miyamoto, 2015	Honshu, Shikoku, Kyushu, Izu Isl.	Intertidal to littoral leaf litter
Nipponorchestia nudiramus Morino and Miyamoto 2015	Tokai, Kinki, Hokuriku districts	Littoral to inland leaf litter
Ezotinorchestia solifuga (Iwasa, 1939)	Hokkaido	Littoral leaf litter
Platorchestia humicola (Martens, 1868)	Honshu	Inland leaf litter
Platorchestia japonica (Tattersall, 1922)	Hokkaido to Okinawa	Lake side, grassland, inland leaf litter
Platorchestia pachypus (Derzhavin, 1937)	Hokkaido to Kyushu	Intertidal
Platorchestia platensis (Krøyer, 1845)	Hokkaido to Okinawa, Ogasawara Isl.	Intertidal
Platorchestia sp. sensu Morino (2015)	Honshu to Kyushu	Inland leaf litter
Pyatakovestia boninensis Morino and Miyamoto, 2015	Hahajima Isl. (Ogasawara Isl.)	Intertidal to inland leaf litter

(continued)

Table 9.1 (continued)

Species	Distribution in Japan	Habitat
Pyatakovestia iwasai Morino and Miyamoto, 2015	Central Honshu to Okinawa	Intertidal to littoral leaf litter
Pyatakovestia pyatakovi (Derzhavin, 1937)	Hokkaido, Honshu, Tsushima Isl.	Intertidal to littoral leaf litter
Sinorchestia nipponensis (Morino, 1972)	Honshu, Shikoku, Kyushu	Intertidal to littoral leaf litter
Sinorchestia sinensis (Chilton, 1925)	Honshu (Kii Peninsula) to Okinawa	Intertidal
Talitroides topitotum (Burt, 1934)	Okinawa	Inland leaf litter
Traskorchestia ochotensis (Brandt, 1851)	Eastern Hokkaido	Intertidal, grassland, littoral leaf litter
Trinorchestia trinitatis (Derzhavin, 1937)	Hokkaido to Kyushu	Intertidal

Eogammarus and *Jesogammarus*, have been recorded. *Eogammarus* is widely distributed in the North Pacific Rim and contains 11 species, 2 of which are known from rivers and lakes in Hokkaido and northern Honshu. *Jesogammarus* is the most divergent freshwater group in Japan; it is found in various freshwater bodies such as spring brooks, mountain streams, and lowland lakes. Twenty species have been recorded from Japan, and there are still several undescribed species in this genus.

Crangonyctids occur in freshwater in many parts of the Holarctic and are especially divergent in North America. In Japan, *Crangonyx floridanus* is recognized as an alien species. This species was introduced from North America in the 1980s and is now widespread in Japan (Morino et al. 2004). In some areas, *C. floridanus* co-occurs with native amphipods (Tomikawa, personal observation).

Gammarids are distributed throughout much of the Holarctic, including both marine and freshwater species, four of which occur in Japan. *Gammarus nipponensis* is the most common freshwater species in western Japan. It is distributed in western Honshu, Shikoku, and Kyushu, with high genetic divergence among regional populations (Hou et al. 2007; Tomikawa et al. 2014b). Other species are limited to narrow areas. *Gammarus koreanus* was originally described by Uéno (1940) based on specimens from the Korean Peninsula. Recently, Tomikawa et al. (2012) recorded this species from the Gotō Islands, Nagasaki Prefecture. *Gammarus mukudai* is distributed in the Iki and Tsushima Islands, Nagasaki Prefecture. The occurrence of *G. sobaegensis* in Japan is under debate (Tomikawa and Morino 2012).

Kamakids inhabit primarily marine and brackish environments with a few freshwater representatives. In Japan, the freshwater species *Kamaka biwae*, *K. kuthae*, and *K. morinoi* have been recorded; the latter two are also found in brackish environments such as river mouths and brackish lakes. *Kamaka biwae* is endemic to Lake Biwa.

Luciobliviidae is currently monospecific, containing *Lucioblivio kozaensis*. This species is recorded from the hyporheic zone, which is a region beneath and alongside a stream bed in Wakayama and Shizuoka Prefectures (Tomikawa et al. 2007b).

Mesogammarids inhabit littoral marine and freshwater habitats. Two interstitial species, *Eoniphargus kojimai* and *Octopupilla felix*, are known in Japan. Previously, the taxonomic affinities of *Eoniphargus* and Indian *Indoniphargus* were unclear. Both genera have been transferred to Mesogammaridae based on molecular data (Tomikawa et al. 2007b).

Although the majority of Pontogeneiidae are marine species, three genera, *Awacaris*, *Relictomoera*, and *Sternomoera*, have been recorded from freshwater environments in Japan. *Awacaris* and *Relictomoera* are monotypic and have been recorded from freshwater caves in Gotō Island (Nagasaki Prefecture) and Tokushima Prefecture, respectively. *Sternomoera* comprises five species, of which two are troglobitic and the others are epigeal. *Sternomoera tsushimana*, one of the troglobitic species, has been transferred from *Relictomoera* to *Sternomoera* (Tomikawa et al. 2014a).

Pseudocrangonyctid amphipods are troglobitic and distributed in Japan, Korea, China, and Russia. This family comprises six species in two genera, *Eocrangonyx* (one species) and *Pseudocrangonyx* (five species), in Japan. Several undescribed species remain. This family is closely related to the Crymostygidae (Sidorov and Gontcharov 2015).

Talitridae consists of terrestrial amphipods, but some species are occasionally found in freshwater. They can jump using their uropods. Japanese talitrid species are classified into the following three ecological types proposed by Bousfield (1982): (1) beachfleas in intertidal and coastal leaf litter; (2) sandhoppers, which are found on sandy beaches and have the ability to sink into the sand; and (3) landhoppers, which are truly terrestrial. *Platorchestia platensis* is recognized as cosmopolitan. However, recent taxonomic studies have divided it into local independent species (Miyamoto and Morino 2004). Revised studies including molecular phylogenetic analyses are needed to clarify the taxonomic status of Japanese *P. platensis*.

9.4 Geographic Distribution

Because freshwater and terrestrial animals cannot cross the sea, straits often act as a geographic barrier to distributional expansion. However, recent biogeographic and phylogeographic studies have revealed that relationships between the formation of straits and the distribution of freshwater and terrestrial gammarids are complicated (Tomikawa et al. 2014b). In this section, recent information on the distributions of freshwater and terrestrial species is introduced.

9.4.1 Freshwater Taxa

The distribution patterns of *Gammarus* in the Japanese Archipelago and the Korean Peninsula are biogeographically interesting. *Gammarus nipponensis* is widely distributed in western Honshu, Shikoku, and Kyushu. *Gammarus mukudai* is limited in its distribution to the Iki and Tsushima Islands. *Gammarus sobaegensis* is widely distributed on the Korean Peninsula. *Gammarus nipponensis*, *G. mukudai*, and *G. sobaegensis* exhibit an allopatric geographic distribution pattern, with the boundaries corresponding to straits located between Kyushu and the Korean Peninsula: the Korea Strait and Iki Strait. These straits form boundaries between *G. sobaegensis* and *G. mukudai*, and between *G. mukudai* and *G. nipponensis*, respectively (Fig. 9.2). Although the water in the Tsushima Strait is deeper than that of the Iki Strait, the former does not form the boundary of any *Gammarus* species distributions. That is, *G. mukudai* is distributed in the Iki and Tsushima Islands spanning the Tsushima Strait. From molecular data, *G. mukudai* from Tsushima Island is not a monophyletic group with high sequence divergence (Tomikawa et al. 2014b). However, *G. mukudai* from Iki Island forms a monophyletic group with low sequence divergence (Tomikawa et al. 2014b). This observation would indicate that *G. mukudai* recently invaded Iki Island from Tsushima Island. Yokoyama et al. (2007) suggested that the sea level around Oki Island (off Shimane Prefecture, Honshu) was approximately 150 m lower during the last glacial maximum (LGM) than at present. According to Ohshima (1990), the Tsushima Strait was closed when the sea level was 110 m lower, indicating that Tsushima Island might have been connected to Iki Island by a land bridge during the LGM if the same sea level change occurred in the Tsushima Strait. Strong glacial epochs occurred approximately 0.78 million years ago (MYA), and after that time, at least five strong glacial periods comparable to the LGM have been reported (Lisiecki and Raymo 2005), which suggests that a land bridge between Tsushima Island and Iki Island was likely formed during that time. Based on Lisiecki and Raymo (2005) and Domitsu et al. (2011), the following land bridge formation times have been estimated for the possible migration of *G. mukudai* from Tshushima Island to Iki Island at approximately 0.676–0.621, 0.478–0.424, 0.374–0.337, 0.191–0.130, and 0.029–0.014 MYA. The correct timing and route of migration should be investigated in future studies.

The Gotō Islands are located off the western coast of Kyushu. As the Gotō Islands were part of Kyushu until about 8500 years ago, when the Gotō Strait separated them (Ohshima 1991), the fauna and the flora of these islands are similar to that of Kyushu. For this reason, the Gotō Strait is not thought to be an important zoogeographic boundary. *Gammarus koreanus* is distributed on China's coasts. Recently, this species was found in the Gotō Islands (Tomikawa et al. 2012). The Gotō Strait is a distributional boundary between *G. koreanus* and *G. nipponensis*. The disjunct distribution of *G. koreanus* may indicate that the Gotō populations are a glacial relict.

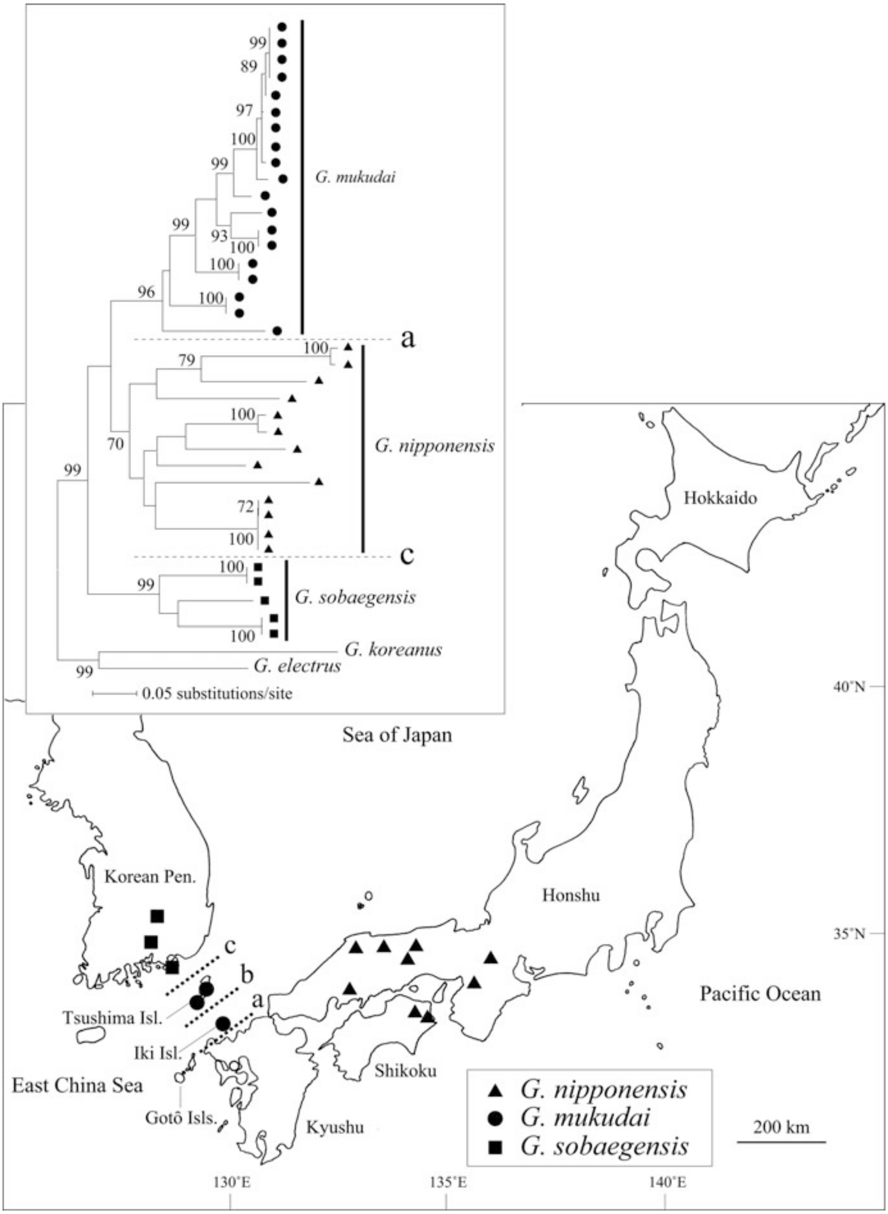

Fig. 9.2 Maximum-likelihood (ML) tree of *Gammarus mukudai*, *G. nipponensis*, and *G. sobaegensis* based on the combined partial sequences of COI and 28S rRNA genes (1177 bp), and geographic distributions of these species. Bootstrap values >50 % are shown. (**a**) Korea Strait. (**b**) Tsushima Strait. (**c**) Iki Strait. (Modified from Tomikawa et al. 2014b)

The Tsugaru Strait is an important hypothetical boundary for birds and animals (Blakiston's Line) that separates the characteristic Hokkaido fauna from that of Honshu. It is thought that the Tsugaru Strait acts as a geographic barrier for freshwater amphipod expansion because they cannot cross the sea. However, *Eogammarus kygi* is widely distributed from Hokkaido to Aomori Prefecture across the Tsugaru Strait (Tomikawa et al. 2006). Similarly, *Jesogammarus jesoensis* and *Pseudocrangonyx yezonis* are also distributed in Hokkaido and Honshu across the Tsugaru Strait. There is no geological evidence for the presence of a land bridge between Hokkaido and Honshu after 16 MYA (Suzaki and Minoura 1992). Whether these species expanded their distributions before the formation of the Tsugaru Strait or dispersed across the strait after it was formed is unknown.

9.4.2 Terrestrial Talitrids

The Tokara Strait is also an important hypothetical boundary for Japanese animals known as Watase's Line. Figure 9.3 roughly shows the talitrid species distribution ranges. The following six types of distributions are recognized: (1) species widely distributed from Hokkaido to Okinawa across the Tsugaru and Tokara Straits, such as *Platorchestia platensis* and *P. japonica* (although there is a possibility that sibling species are included in the former species); (2) species distributed south of the Tsugaru Strait (across the Tokara Strait), for example, *Sinorchestia sinensis*, *Pyatakovestia iwasai*, and *Platorchestia* sp.; (3) species distributed between south of the Tsugaru Strait and north of the Tokara Strait, such as *Sinorchestia nipponensis*, *Nipponorchestia curvatus*, *N. nudiramus*, *Mizuhorchestia urospina*, and *Platorchestia humicola*; (4) species distributed north of the Tokara Strait (across the Tsugaru Strait), for example, *Platorchestia pachypus*, *Pyatakovestia pyatakovi*, *Trinorchestia trinitatis*, and *Kokuborchestia kokuboi*; (5) species distributed north of the Tsugaru Strait, such as *Ezotinorchestia solifuga*, *Traskorchestia ditmari*, and *T. ochotensis*; and (6) species in restricted distribution ranges, for example, *Bousfieldia omoto* endemic to the Ishigaki and Iriomote Islands, *Minamitalitrus zoltani* endemic to Minamidaitō Island, *Pyatakovestia boninensis* endemic to the Ogasawara Islands, and *Talitroides topitotum* from Okinawa Island (widely distributed in subtropical regions).

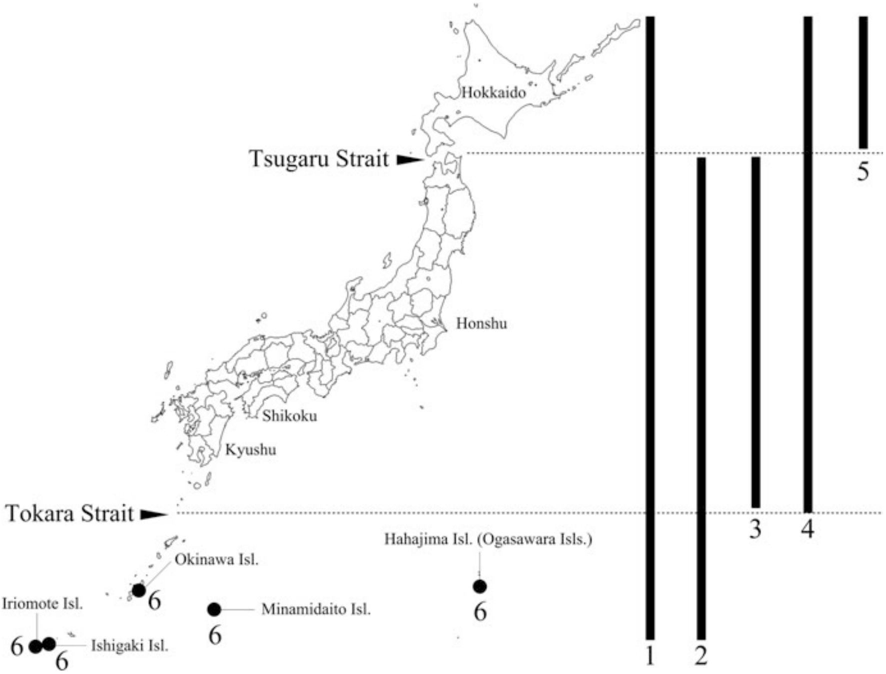

Fig. 9.3 Six types of distributional ranges of Talitridae

9.5 Adaptation and Diversification

9.5.1 Adaptation to and Invasion of Different Salinity Environments

Gammaridean amphipods occur in aquatic environments of varying salinity, including marine, brackish, and freshwater. It is generally accepted that freshwater amphipods evolved from marine ancestors and are polyphyletic (Barnard and Barnard 1983; Väinölä et al. 2008). Tomikawa et al. (2010) analyzed the molecular phylogenetic relationships among Japanese amphipods from various aquatic environments, and indicated that none of the marine, brackish, or freshwater species formed monophyletic group (Fig. 9.4). Therefore, it is likely that invasions from marine to freshwater environments have occurred independently in different lineages. Hou et al. (2011) revealed that the Holarctic genus *Gammarus* originated from a saline ancestor that inhabited the Tethyan region, suggesting that habitat shifts from saline to freshwater increased the diversification rate.

Osmoregulation is an important function in maintaining internal environment constancy. The first studies on osmoregulation in aquatic organisms were carried out on fish. These studies identified that ionocytes (= chloride cells) in the gill epithelium have an important function in osmoregulation (Sakamoto et al. 2001).

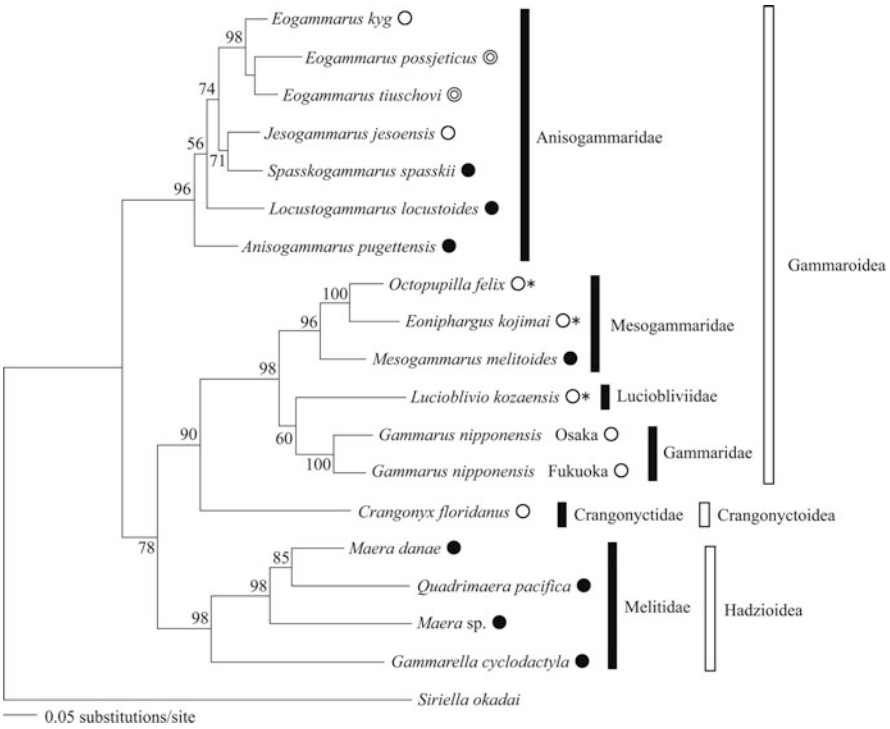

Fig. 9.4 ML tree of selected Japanese gammaridean species based on the combined partial sequences of 16S rRNA and 28S rRNA genes (591 bp). Bootstrap values >50 % are shown. *Black circles* indicate marine species, *double circles* indicate brackish water species, *open circles* indicate freshwater species, and asterisks indicate interstitial species. *Black and white vertical bars* to right of species names indicate families and superfamilies, respectively. (Modified from Tomikawa et al. 2010)

Ionocytes are morphologically characterized by abundant mitochondria and develop folded epithelia. Amphipod coxal gills are composed of one type of epithelial cell, which are identical in microstructure among different amphipods (Kikuchi 1992). Using transmission electron microscopy and histological observations with the mitochondrial dye DASPEI, a cell type was discovered in amphipod coxal gills and sternal epithelia that is morphologically similar to fish ionocytes (Kikuchi 1992; Matsumasa et al. 1998; Tomikawa and Mukuda 2010). Therefore, it is likely that coxal gills and sternal epithelia are the site of osmoregulation in amphipods. In freshwater and brackish water amphipods, ionocytes have numerous mitochondria, indicating that they actively take ions into the cell from the ambient water against a concentration gradient. However, marine amphipod ionocytes only have a few mitochondria, indicating the absence of osmoregulation (Kikuchi 1992). More detailed investigations into functional ionocyte morphology is needed to determine adaptive radiation to different salinity environments in gammaridean amphipods.

9.5.2 Groundwater Invasions

It is believed that troglobitic amphipods may have evolved from either epigean freshwater or marine ancestors. Pseudo-crangonyctids are common in Japanese groundwater. Because the family does not have close phylogenetic affinities with any marine taxa, it is though that this family may be derived from freshwater ancestors that invaded from epigean waters (Holsinger 1989). Rich amphipod diversity in interstitial waters has recently been revealed in Japan (Tomikawa et al. 2007b, 2014a). *Octopupilla felix*, *Lucioblivio kozaensis*, and *Sternomoera morinoi* were newly discovered, and *Eoniphargus kojimai* was reported for the first time since its original description almost 50 years ago (Tomikawa et al. 2007b, 2014a). Molecular data suggest that invasions into groundwater habitats have occurred independently in different lineages (Tomikawa et al. 2010) (Fig. 9.4). The congeners of *S. morinoi* are epigean freshwater species. Tomikawa et al. (2014a) revealed that *S. morinoi* is sister to all the other species in the *Sternomoera* molecular phylogenetic tree. Because almost all the members of the related genus *Paramoera* are marine, an initial invasion from the sea through interstitial waters has been suggested.

In general, troglobitic amphipods are characterized by either the loss or rudimentation of eyes and pigment, attenuation of the body or appendages, and development of surface setae. These morphological features are probably adaptation for life in a subterranean environment.

9.5.3 Origin of Migration

Migration between freshwater and the sea is known in various groups of aquatic animals. However, there are few amphipods that have migratory life cycles. Kuribayashi et al. (2006) reported the catadromous migration of *Sternomoera rhyaca*. This species inhabits freshwater for most of its life cycle, but undertakes a short catadromous migration to the sea for reproduction. Kuribayashi et al. (2006) proposed two hypotheses for the origin of the migratory life cycle in *S. rhyaca*: (1) migration evolved independently in *S. rhyaca* from a completely freshwater adapted ancestor; and (2) migration is an intermediate stage in the evolutionary adaptation to freshwater from a marine or migratory estuarine ancestor. Recently, Tomikawa et al. (2014a) investigated the molecular phylogenetic relationships among Japanese species of *Sternomoera*. In the phylogenetic tree, the stygobiont *S. morinoi* appears to have diverged first from a common ancestor of *Sternomoera*, which supports the former hypothesis for the origin of *S. rhyaca* migration proposed by Kuribayashi et al. (2006).

9.6 Introduced Species

Crangonyx floridanus is an invasive species from North America. This species was first discovered from a pond in Chiba Prefecture in 1989 (Morino et al. 2004). *Crangonyx. floridanus* has subsequently spread throughout Japan, and has been recorded in 28 prefectures to date (Kanada et al. 2007). Because *C. floridanus* is more tolerant of water pollution and hypoxia than native Japanese freshwater amphipods, it is feared that the species is affecting the local ecosystem by competing with native species.

Jesogammarus suwaensis and *J. naritai* have been considered sister species because of similarities in their morphology and habitat preferences. The former is endemic to Lake Biwa, whereas the latter inhabits Lake Suwa, Nagano Prefecture, and Lake Kawaguchi, Yamanashi Prefecture. However, molecular and morphological data suggest that they are likely to be the same species (Tomikawa et al. 2007a). Because many edible freshwater organisms have been artificially transplanted from Lake Biwa to Lakes Suwa and Kawaguchi, *J. naritai* might have been accidentally transported from the former to the latter lakes (Tomikawa et al. 2007a).

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References

Akatsuka K, Komai T (1922) *Pseudocrangonyx*, a new genus of subterranean amphipods from Japan. Annot Zool Jpn 10:119–126

Ariyama H (1996) Four species of the genus *Grandidierella* (Crustacea: Amphipoda: Aoridae) from Osaka Bay and the northern part of the Kii Channel, Central Japan. Publ Seto Mar Biol Lab 37:167–191

Ariyama H (2004) Nine species of the genus *Aorides* (Crustacea: Amphipoda: Aoridae) from Osaka Bay, Central Japan. Publ Seto Mar Biol Lab 40:1–66

Ariyama H (2005) Six species of the genus *Colomastix* (Crustacea: Amphipoda: Colomastigidae) from Western Japan, with descriptions of two new species. Bull Osaka Mus Nat Hist 59:1–40

Barnard JL, Barnard KH (1983) Freshwater Amphipoda of the world, Part I, Evolutionary Patterns. Part II, Handbook and Bibliography. Hayfield Associates, Mt. Vernon

Barnard JL, Ingram C (1990) Lysianassoid Amphipoda (Crustacea) from deep-sea thermal vents. Smithson Contrib Zool 499:1–80

Bousfield EL (1978) A revised classification and phylogeny of amphipod crustaceans. Trans R Soc Can Ser 4(16):343–390

Bousfield EL (1982) The amphipod superfamily Talitroidea in the Northeastern Pacific region. 1. Family Talitridae; systematics and distributional ecology. Natl Mus Can Publ Biol Oceanogr 11:1–72

Bulycheva A (1936) New species of Amphipoda from the Japan Sea. Ann Mag Nat Hist Ser 10(18):242–256

Dahl E (1944) Amphipoda of the family Ampeliscidae from Professor Sixton Boek's expedition to Japan, 1914. Ark Zool 36A(1):1–18

Domitsu H, Uchida J, Ogane K, Dobuchi N, Sato T, Ikehara M, Nishi H, Hasegawa S, Oda M (2011) Stratigraphic relationships between the last occurrence of *Neogloboquadrina inglei* and marine isotope stages in the Northwest Pacific, D/V Chikyu Expedition 902, Hole C9001C. Newsl Stratigr 44(2):113–122

Gamô S (1981) A new deep-sea Amphipoda, *Lepechinella sagamiensis* sp. nov. from Sagami Bay. Proc Jpn Soc Syst Zool 20:16–20

Hirayama A (1983) Taxonomic studies on the shallow water gammaridean Amphipoda of West Kyushu, Japan. I. Acanthonotozomatidae, Ampeliscidae, Amphithoidae, Amphilochidae, Anamixidae, Argissidae, Atylidae and Colomastigidae. Publ Seto Mar Biol Lab 28:75–150

Hirayama A (1988) Taxonomic studies on the shallow water gammaridean Amphipoda of West Kyushu, Japan. VIII. Pleustidae, Podoceridae, Priscomilitaridae, Stenothoidae, Synopiidae, and Urothoidae. Publ Seto Mar Biol Lab 33:39–77

Hiwatari T (2003) Taxonomic study on *Hyale* (Crustacea, Amphipoda, Hyalidae) from the coast of Japan and adjacent waters. Publ Seto Mar Biol Lab 39:229–262

Hiwatari T, Kajihara T (1981a) Taxonomy of the family Hyalidae (Amphipoda, Crustacea) in Japan. I. Three new species of the genus *Hyale*. Proc Jpn Soc Syst Zool 20:21–34

Hiwatari T, Kajihara T (1981b) Taxonomy of the family Hyalidae (Amphipoda, Crustacea) in Japan. II. A new species of the genus *Hyale*. Proc Jpn Soc Syst Zool 21:35–40

Holsinger JR (1989) Allocrangonyctidae and Pseudocrangonyctidae, two new families of Holarctic subterranean amphipod crustaceans (Gammaridea), with comments on their phylogenetic and zoogeographic relationships. Proc Biol Soc Wash 102:947–959

Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Daneliya M, Dauvin J-C, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Holsinger J, Hughes L, Jazdzewski K, Just J, Kamaltynov RM, Kim Y-H, King R, Krapp-Schickel T, LeCroy S, Lörz A-N, Senna AR, Serejo C, Sket B, Tandberg AH, Thomas J, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2015) World Amphipoda database. http://www.marinespecies.org/amphipoda. Accessed 19 Oct 2015

Hou Z, Fu J, Li S (2007) A molecular phylogeny of the genus *Gammarus* (Crustacea: Amphipoda) based on mitochondrial and nuclear gene sequences. Mol Phylogenet Evol 45:596–611

Hou Z, Sket B, Fišer C, Li S (2011) Eocene habitat shift from saline to freshwater promoted Tethyan amphipod diversification. Proc Natl Acad Sci USA 108:14533–14538

Ishimaru S (1984) Taxonomic studies of the family Pleustidae (Crustacea, Amphipoda, Gammaridea) from coastal waters of Northern Japan. I. The genus *Parapleustes*. J Fac Sci Hokkaido Univ Ser VI Zool 23:403–453

Ishimaru S (2001) Development of Amphipoda systematics: recent trends. Kaiyo 26:15–20 [in Japanese]

Iwasa M (1939) Japanese Talitridae. J Fac Sci Hokkaido Imp Univ Ser VI Zool 6(4):255–296

Kanada S, Kuranishi RB, Ishiwata S, Tojo K, Shimizu T, Taira H, Satake K (2007) Distribution of an alien species, *Crangonyx floridanus* Bousfield (Crustacea: Amphipoda: Crangonyctidae) in Japan. Jpn J Limnol 68:449–460

Kikuchi S (1992) Ultrastructure of the crustacean gill epithelia and the environmental salinities. Comp Physiol Biochem 9:129–140 (in Japanese)

Kuribayashi K, Mawatari SF, Ishimaru S (1996) Taxonomic study on the genus *Sternomoera* (Crustacea: Amphipoda), with redefinition of *S. japonica* (Tattersall, 1922) and description of a new species from Japan. J Nat Hist 30:1215–1237

Kuribayashi K, Katakura H, Kyono M, Dick MH, Mawatari SF (2006) Round-trip catadromous migration in a Japanese amphipod, *Sternomoera rhyaca* (Gammaridea: Eusiridae). Zool Sci 23: 763–774

Lisiecki LE, Raymo ME (2005) A Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. Paleoceanography 20:1–17

Lowry JK, Myers AA (2013) A phylogeny and classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). Zootaxa 3610:1–80

Martens E (1868) Ueber einige ostasiatishe Süsswasserthire. Arch Naturg 34:1–64

Matsumasa M, Kikuchi S, Takeuchi I (1998) Specialized ion-transporting epithelium around the blood vessel of the coxal gills in a deep-sea amphipod, *Eurythenes gryllus*. J Crust Biol 18: 686–694

Meland K, Willassen E (2007) The disunity of "Mysidacea" (Crustacea). Mol Phylogenet Evol 44: 1083–1104

Miyamoto H, Morino H (2004) Taxonomic studies on the Talitridae (Crustacea, Amphipoda) from Taiwan. II. The genus *Platorchestia*. Publ Seto Mar Biol Lab 40:67–96

Morino H (1985) Revisional studies on *Jesogammarus–Annanogammarus* group (Amphipoda: Gammaroidea) with descriptions of four new species from Japan. Publ Itako Hydrobiol Station 2:9–55

Morino H (2015) Amphipoda. In: Aoki J (ed) Pictorial keys to soil animals of Japan, 2nd edn. Tokai University Press, Hadano, pp 1069–1089 (in Japanese)

Morino H, Miyamoto H (2015) A new land-hopper genus, *Nipponorchestia*, with two new species from Japan (Crustacea, Amphipoda, Talitridae). Bull Natl Mus Nat Sci Ser A 41:1–13

Morino H, Kusano H, Holsinger JR (2004) Description and distribution of *Crangonyx floridanus* (Crustacea: Amphipoda: Crangonyctidae) in Japan, an introduced freshwater amphipod from North America. Contrib Biol Lab Kyoto Univ 29:371–381

Myers AA, Lowry JK (2003) A phylogeny and a new classification of the Corophiidea Leach, 1814 (Amphipoda). J Crust Biol 23:443–485

Nagata K (1965a) Studies on marine gammaridean Amphipoda of the Seto Inland Sea. I. Publ Seto Mar Biol Lab 13:131–170

Nagata K (1965b) Studies on marine gammaridean Amphipoda of the Seto Inland Sea. II. Publ Seto Mar Biol Lab 13:171–186

Nagata K (1965c) Studies on marine gammaridean Amphipoda of the Seto Inland Sea. III. Publ Seto Mar Biol Lab 13:291–326

Ohshima K (1990) The history of straits around the Japanese Islands. Quat Res 29:193–208 (in Japanese with English summary)

Ohshima K (1991) The late-quaternary sea-level change of the Japanese Islands. J Geogr 100: 967–975 (in Japanese)

Sakamoto T, Uchida K, Yokota S (2001) Regulation of the ion-transporting mitochondrion-rich cell during adaptation of teleost fishes to different salinities. Zool Sci 18:1163–1174

Serejo CS, Lowry JK (2008) The coastal Talitridae (Amphipoda: Talitroidea) of Southern and Western Australia, with comments on *Platorchestia platensis* (Krøyer, 1845). Rec Aust Mus 60:161–206

Sidorov DA, Gontcharov AA (2015) Preliminary analysis of phylogenetic relationships of the Asian-Pacific endemial subterranean amphipod genus *Pseudocrangonyx* among families and genera of crangonyctoidean amphipods inferred by partial LSU rDNA. Zool Sci 32:178–182

Spears T, DeBry RW, Abele LG, Chodyla K (2005) Peracarid monophyly and interordinal phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea: Malacostraca: Peracarida). Proc Biol Soc Wash 118:117–157

Stebbing TRR (1888) Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–1876. Rep Sci Challenger Zool 29:1–1737

Stephensen K (1932) Some new amphipods from Japan. Annot Zool Jpn 10:119–126

Stephensen K (1933) *Ceinina japonica* (n. gen., n. sp.), a new aberrant species of the amphipodan family Talitridae from Japan. Trans Sapporo Nat Hist Soc 13:63–68

Stephensen K (1938) *Grandidierella japonica* n. sp. a new amphipod with stridulating organs from brackish water in Japan. Annot Zool Jpn 17:179–184

Stephensen K (1944) Some Japanese amphipods. Vidensk Med Naturh Foren 108:25–88

Suzaki T, Minoura K (1992) Stratigraphy and paleogeographic reconstruction of the Upper Cenozoic in the Aomori district, northern Japan. Mem Geol Soc Jpn 37:5–37 (in Japanese with English summary)

Tattersall WM (1922) Zoological results of a tour in the Far East. Part 8. Amphipoda with notes on an additional species of Isopoda. Mem Asiat Soc Bengal 6:435–459

Tomikawa K, Morino H (2012) An annotated inventory with a key to freshwater Amphipoda (Crustacea) from Japan. Taxa 32:39–51 (in Japanese with English summary)

Tomikawa K, Mukuda T (2010) Detection of osmoregulatory region of Amphipoda (Crustacea) using DASPEI. Bull Biogeogr Soc Jpn 65:135–139 (in Japanese with English summary)

Tomikawa K, Morino H, Toft J, Mawatari SF (2006) A revision of *Eogammarus* Birstein, 1933 (Crustacea, Amphipoda, Anisogammaridae), with a description of a new species. J Nat Hist 40: 1083–1148

Tomikawa K, Kobayashi N, Morino H, Hou Z, Mawatari SF (2007a) Phylogenetic relationships within the genus *Jesogammarus* (Crustacea, Amphipoda, Anisogammaridae) deduced from mitochondrial COI and 12S sequences. Zool Sci 24:173–180

Tomikawa K, Kobayashi N, Morino H, Mawatari SF (2007b) New gammaroid family, genera and species from subterranean waters of Japan, and their phylogenetic relationships (Crustacea: Amphipoda). Zool J Linn Soc 149:643–670

Tomikawa K, Kobayashi N, Mawatari SF (2010) Phylogenetic relationships of superfamily Gammaroidea (Amphipoda) and its allies from Japan. Crust Res 39:1–10

Tomikawa K, Tashiro S, Kobayashi N (2012) First record of *Gammarus koreanus* (Crustacea, Amphipoda, Gammaroidea) from Japan, based on morphology and 28S rRNA gene sequences. Species Divers 17:39–48

Tomikawa K, Kobayashi N, Kyono M, Ishimaru S, Grygier MJ (2014a) Description of a new species of *Sternomoera* (Crustacea: Amphipoda: Pontogeneiidae) from Japan, with an analysis of the phylogenetic relationships among the Japanese species based on the 28S rRNA gene. Zool Sci 31:475–490

Tomikawa K, Soh HY, Kobayashi N, Yamaguchi A (2014b) Taxonomic relationship between two *Gammarus* species, *G. nipponensis* and *G. sobaegensis* (Amphipoda: Gammaridae), with description of a new species. Zootaxa 3873:451–476

Uéno M (1927) Notes on some subterranean isopods and amphipods of Japan. Mem Coll Sci Kyoto Imp Univ Ser B 3:355–368

Uéno M (1940) Some freshwater amphipods from Manchoukuo, Corea and Japan. Bull Biogeogr Soc Jpn 10:63–85

Uéno M (1971) A new cave amphipod Crustacea from Japan. Int J Speleol 3:241–247

Väinölä R, Witt JDS, Grabowski M, Bradbury JH, Jazdzewski K, Sket B (2008) Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. Hydrobiologia 595:241–255

White KN, Reimer JD (2012) Commensal Leucothoidae (Crustacea, Amphipoda) of the Ryukyu Archipelago, Japan. Part I: Ascidian-dwellers. ZooKeys 163:13–55

Yamato S (1990) Two new species of the genus *Melita* (Crustacea: Amphipoda) from shallow waters of the Seto Inland Sea of Japan. Publ Seto Mar Biol Lab 34:149–165

Yokoyama Y, Kido Y, Tada R, Minami I, Finkel RC, Matsuzaki H (2007) Japan Sea oxygen isotope stratigraphy and global sea-level changes from the Oki Ridge. Palaeogeogr Palaeoclimatol Palaeoecol 247:5–17

Chapter 10
Tardigrade Research in Japan

Atsushi C. Suzuki

Abstract Tardigrades (water bears) are microscopic animals walking slowly with four pairs of legs, comprising the phylum Tardigrada, which is closely related to other ecdysozoans such as Arthropoda and Onychophora. They dwell in diverse habitats such as terrestrial soil, mosses, lichens, and sediments in freshwater and marine environments. Limno-terrestrial tardigrades show characteristic biological properties including anhydrobiosis, in which the animals can tolerate extreme conditions. Freshwater and marine species have been less studied than terrestrial species. However, biodiversity research on Japanese marine tardigrades became active after 2013. In this chapter, studies on tardigrades in Japan are briefly reviewed. A total of 166 species known from Japan are listed.

Keywords Tardigrada • Taxonomy • Checklist • Review • Biogeography • Meiofauna • Terrestrial invertebrates • Freshwater • Marine meiobenthos

10.1 Brief Summary on Tardigrades

Tardigrada is a phylum with minute microscopic animals, commonly referred to as water bears, found among the meiofauna, walking slowly with four pairs of legs. The body has a head segment and four trunk segments with paired legs. They have been found among diverse habitats such as terrestrial soil, moss and lichen, and sediments from freshwater, as well as from marine environments. Goeze (1773) described the "kleine Wasserbär," a freshwater tardigrade from duckweed leaves. He named it after its appearance and wrote that everyone who looks at it once under the microscope will recognize this name. Three years after this discovery, Spallanzani (1776) carried out several experiments with "tardigrado," obtained from roof dust, to show their anhydrobiosis ability and high-temperature tolerance. The name of his animal derived from its slow movement. This terrestrial tardigrade was later considered as *Milnesium tardigradum* Doyère, 1840 (see Doyère 1840;

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Marcus 1929). The first binominally described tardigrade was *Acarus ursellus* Müller, 1785, which was placed in Acari (mites and ticks, in the modern classification, in the phylum Arthropoda), but the earliest valid name at present is *Macrobiotus hufelandi* Schultze, 1834, which was also treated as an arthropod, belonging to Isopoda this time. However, the tardigrade body plan shows unique characteristics enough to be distinguished from Arthropoda. Therefore, Ramazzotti (1962) elected a new phylum, Tardigrada, for this group of animals. More than 1200 species are already known in this phylum so far, and taxonomists continue to add a number of new species every year. Therefore, there are not any monographs covering the entire phylum after Ramazzotti and Maucci (1983), but the tardigrade checklist (Guidetti and Bertolani 2005; Degma and Guidetti 2007) has been repeatedly revised, and the most recent version (Degma et al. 2015) is found through the website (http://www.tardigrada.modena.unimo.it).

Three classes have been recognized in Tardigrada: Heterotardigrada, Mesotardigrada, and Eutardigrada. Heterotardigrada consists of two orders, Arthrotardigrada and Echiniscoidea. All members of Arthrotadigrada and one family, Echiniscoididae, in Echiniscoidea are marine. The other three families in Echiniscoidea and the two classes Mesotardigrada and Eutardigrada are all limnoterrestrial tardigrades except for a few eutardigrades having returned to the marine environment from the land. The constitution of this phylum as of this writing (December 2015) is summarized in Table 10.1.

10.2 Beginning of Tardigrade Research in Japan

Iijima (1889) was probably the first Japanese author who referred to tardigrades in his textbook of zoology (also see Iijima 1918), followed by several authors who briefly reviewed the animal in the early twentieth century (Okamura 1908; Kishida 1910, 1927; Kawamura 1918). Esaki (1930) described this taxon in detail. However, the research on Japanese tardigrades had been very limited until the first half of the twentieth century. The first tardigrade found from Japan was *Echiniscus elegans* Richters, 1907, which was described from a moss sample collected in Nagasaki and sent to Germany (Richters 1907). After 30 years from this article, two German authors reported Japanese tardigrades. Mathews (1936–1937) recorded 16 species from Japanese moss samples sent to Beijing where both of them stayed at that time. The other researcher, Rahm, went to Nagasaki in May 1937 and found a new species from a hot spring in Unzen National Park (Rahm 1937b, c). Because this species, *Thermozodium esakii* Rahm, 1937, showed intermediate traits between Heterograda and Eutardigrada, a new order (now recognized as a class), Mesotardigrada, was established. Rahm (1937b, c) also included a brief note on Japanese tardigrades with strong criticism against Mathew's doubtful identification ability.

Kuniyasu Morikawa (1919–2009) was the earliest Japanese soil zoologist who described a new species, *Echiniscus japonicus* Morikawa, 1951 (Fig. 10.1f), with

Table 10.1 Tardigrade taxa and their constituents as of 2015

Class, order, family	Numbers[b] of genera	Species	Japanese records[c]
HETEROTARDIGRADA			
Arthrotardigrada (183 species)			
Archechiniscidae	1	4	–
Batillipedidae	1	28	1/3
Coronarctidae	2	8	1/1
Halechiniscidae	30	109	11/15
Neoarctidae	1	1	–
Renaudarctidae	1	2	1/1
Stygarctidae	8	31	4/8
Echiniscoidea (287 species)			
Echiniscoididae	2	19	1/1
Carphaniidae	1	1	–
Oreellidae	1	3	–
Echiniscidae	14	264	4/37
MESOTARDIGRADA			
Thermozodia (1 species)	1	1	1/1
EUTARDIGRADA			
Apochela (32 species)			
Milnesiidae	4	32	1/1
Parachela (724 species)			
Eohypsibiidae	3	12	2/2
Calohypsibiidae	1	5	1/1
Hypsibiidae	14	156	8/42
Microhypsibiidae	2	5	1/2
Ramazzottiidae	4	36	1/5
Isohypsibiidae	13	209	4/25
Macrobiotidae	19	273	6/17
Murrayidae	3	26	2/4
Necopinatidae	1	1	–
Beornidae[a]	1	1	–

[a] Fossil taxon

[b] The numbers were counted from the *Actual Checklist of Tardigrade Species* ver. 29 (Degma et al. 2015)

[c] The numbers of genera/species (only including those with specific names) recorded from Japan

three other species from Mt. Sara and Mt. Ishizuchi in Shikoku Island (Morikawa 1951a). In the same year, he also published another article (Morikawa 1951b) on a marine tardigrade, *Echiniscoides sigismundi* (M. Schultze, 1865). After a brief review on the systematic problems of tardigrades (Morikawa 1957) he published a comprehensive review of tardigrade studies (Morikawa 1967), which has long been the only monograph on Tardigrada written in Japanese. Recently, however, there are also several reports on tardigrades for general Japanese readers (Suzuki 2006; Suzuki and Moriyama 2008; Horikawa 2014, 2015).

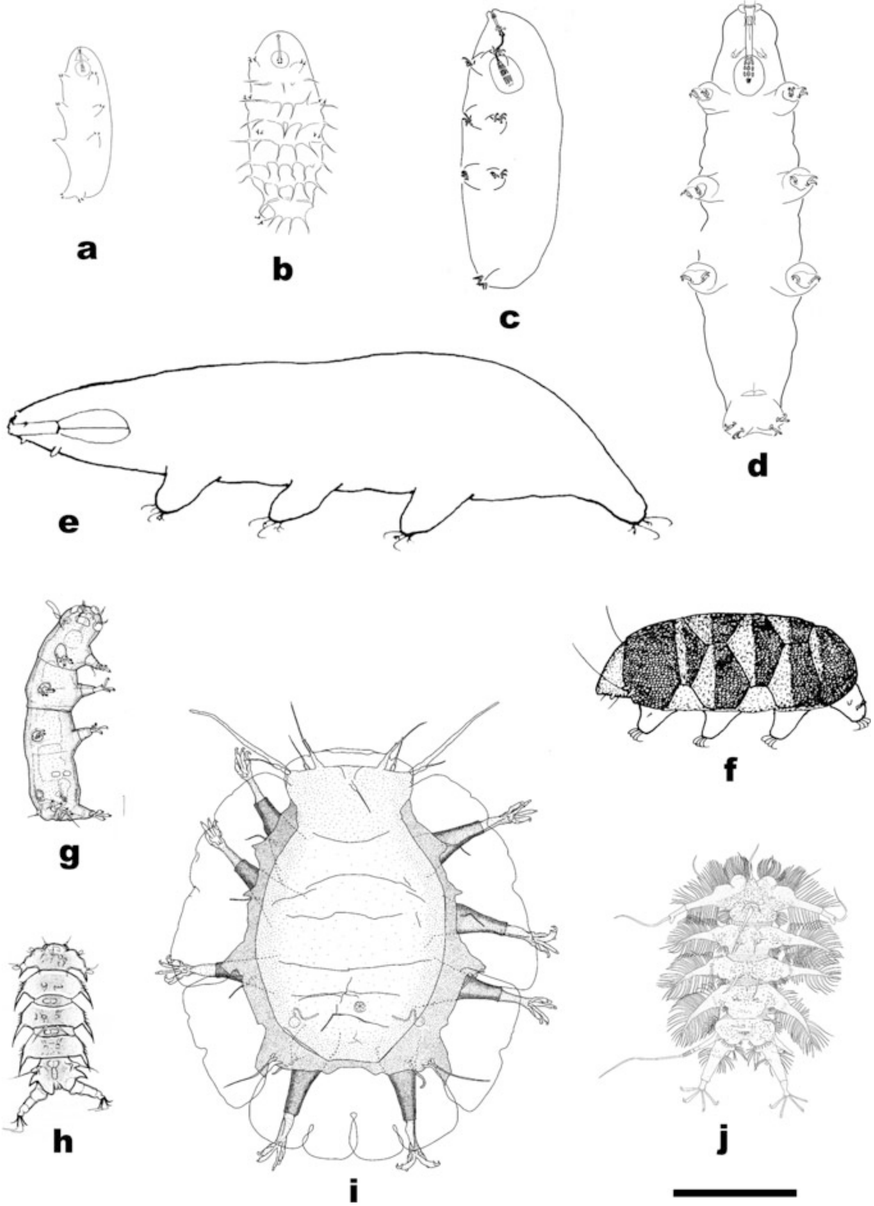

Fig. 10.1 Various Japanese tardigrades. (**a**) *Microhypsibius japonicus*; (**b**) *Calohypsibius ornatus*; (**c**) *Diphascon bidropion*; (**d**) *Calcarobiotus imperialis*; (**e**) *Milnesium* cf. *tardigradum*; (**f**) *Echiniscus japonicus*; (**g**) *Angursa clavifera*; (**h**) *Stygarctus spinifer*; (**i**) *Florarctus wunai*; (**j**) *Neostygarctus lovedeluxe*. **a**, **b** from Ito (1991a); **c** from Ito (1995); **d** from Abe and Takeda (2000a); **e** from Utsugi (1994a); **f** from Morikawa (1951a); **g** from Noda (1985); **h** from Hiruta (1985); **i** from Fujimoto (2015a); **j** from Fujimoto and Miyazaki (2014). *Bar* 100 μm

10.3 Limno-terrestrial Tardigrades

Hatai (1956) recorded eight species of eutardigrades using his unique method to collect tardigrades from dry bamboo leaves. Hatai (1959) studied the distribution of *Milnesium tardigradum* (Fig. 10.1e), discussing its relationship with bamboo species. Watanabe et al. (1961) also studied tardigrades collected by the same method; but after these reports, further research employing this method has not appeared in published articles except that by Nonogaki and Gamô (1989).

A series of nationwide studies of terrestrial tardigrades from urban moss samples (below 500 m a.s.l.) by Utsugi (1985a, b, 1986, 1987, 1988, 1990a, 1991, 1992b, 1993b, 1994a, 1996) revealed various aspects of its distribution in the urban cities of Japan. Utsugi et al. (1997) studied the tardigrade fauna in Toyama Prefecture with regard to the altitude and moss species, showing some tendency of tardigrade preference for moss habitat. There are also several faunistic studies in other areas as follows: Tokyo University Forest in Chiba Prefecture (Ito 1991b), the northern slope of Mt. Fuji (Ito 1991a, 1993, 1995, 1997, 1999), Tanzawa Mountains (Ito and Abe 1997), Oda-Miyama Valley (Ito and Abe 2000), Yatsugatake Mountains (Ito and Abe 2001), the woods in the Imperial Palace (Abe and Takeda 2000b), the woods in Tokiwamatsu Villa (Abe and Takeda 2005), and Kochi Prefecture (Ishida and Matsui 2007).

Freshwater tardigrades have not been so much studied as terrestrial species, although Kawamura (1918) has already shown a figure of *Dactylobiotus macronyx* (Dujardin, 1851) from Lake Biwa. Three species were newly described from Tama River (Sudzuki 1975). Ito and Tagami (1993) found a new species from a swimming pool of Tsukuba University (Ibaraki Prefecture). Among many lakes in Japan, Lake Biwa is still the only lake so far found in the literature with a tardigrade record of 14 species (including 1 endemic) in 7 genera (Biserov et al. 2001).

There are a few ecological analyses. Ito (1999) studied the distribution of terrestrial tardigrades in various forests in central Japan and showed that species in *Macrobiotus* prefer a wide variety of habitats; *Diphascon* species prefer moist habitats, and *Echiniscus* species prefer relatively dry habitats on trees. *Diphascon* are very rare in moss and lichen (Ito and Utsugi 1992). Ito and Abe (2001) showed the soil depth distribution pattern of tardigrades in a subalpine coniferous forest of Mt. Yatsugatake. Harada and Ito (2006) studied the relationship between parameters of soil environment and their inhabitants. Tardigrades have been shown to be parasitized by some fungi (Saikawa and Oyama 1992; Saikawa et al. 1991).

Researches with cultured strains of limno-terrestrial tardigrades have been recently activated to elucidate their life history traits and the mechanism of cryptobiosis, using *Milnesium* sp. originated from Yokohama (Suzuki 2003, 2006, 2008), *Ramazzotius varieornatus* originated from Sapporo (Horikawa et al. 2008, 2012, 2013; Yamaguchi et al. 2012; Tanaka et al. 2015), and *Acutuncus antarcticus* originated from an ice-free area near Showa Station in East Antarctica (Kagoshima et al. 2013; Tsujimoto et al. 2015, 2016).

10.4 Marine Tardigrades Along the Japanese Coast

Despite the rich marine fauna around Japan, the diversity of marine tardigrades has not been fully elucidated. Sudzuki (1979) mentioned a marine species from Taketomi Island without precise description. The first described species was *Hypsibius itoi* Tsurusaki, 1980, now *Thulinius itoi* (see Kaczmarek and Michalcyzk 2006), found from Ishikari Bay; this is apparently one of the few secondary marine residents from a limno-terrestrial genus. Three arthrotardigrades were subsequently described: *Stygarctus spinifer* Hiruta, 1985 from Kushiro (Fig. 10.1h), *Angursa clavifera* Noda, 1985 (Fig. 10.1g), and *Florarctus glareolus* Noda, 1987 from Tanabe Bay. For long only these four species were described originally from the Japanese coast until the description of *Tanarctus diplocerus* Fujimoto et al., 2013 as the fifth species. Marine tardigrade research in Japan is still at the beginning stage, and new species are being described in succession (Fujimoto and Miyazaki 2013; Fujimoto 2014, 2015a, b).

10.5 Tardigrade Diversity in Japan

Twenty-six tardigrade species (9 marine, 17 terrestrial) were so far originally described from Japan, and 166 species had been recorded with specific names up to 2015. Old records, especially those that appeared only once, should be reconfirmed with new specimens. There are also several ‘cosmopolitan’ species necessary to reexamine by more detailed morphological information with molecular analysis. For example, the DNA analysis of *Milnesium* with COI and ITS2 sequences revealed that there are actually three clades, which might be treated as different species of this genus in Japan (Kume et al. 2012). Therefore, there must be many cryptic species even in well-studied urban mosses. The Japanese tardigrades at present with each reference are shown in the following list, which also includes several records once recognized as *species inquirendae* (signified with an asterisk before the species name), and those having only generic names. The species names not appearing in the recent checklist (Degma et al. 2015) are shown without numbers.

Class HETEROTARDIGRADA Marcus, 1927
Order ARTHROTARDIGRADA Marcus, 1927
Family BATILLIPEDIDAE Ramazzotti, 1962

1. *Batillipes pennaki* Marcus, 1946: Noda (1994a, b)
2. *Batillipes similis* Schulz, 1955: Noda (1994a, b), Suzuki (2010)
3. *Batillpes tridentatus* Pollock, 1989: Abukawa (2010)

Family CORONARCIDAE Renaud-Mornant, 1974

4. *Coronarctus* cf. *stylisetus* Renaud-Mornant, 1987: Noda (1989)

Family HALECHINISCIDAE Thulin, 1928
Subfamily DIPODARCTINAE Pollock, 1995

5. *Dipodarctus borrori* Pollock, 1995: Noda (1998)
   Dipodarctus sp.: Fujimoto (2015a)

Subfamily FLORACTINAE Renaud-Mornant, 1982

6. *Florarctus wunai* Fujimoto, 2015 (Fig. 10.1i): Fujimoto (2015a)
7. *Florarctus glareolus* Noda, 1987: Noda (1987)
   Wingstrandarctus sp.: Noda (1994a, b)

Subfamily HALECHINISCINAE Thulin, 1928

8. *Halechiniscus churakaagii* Fujimoto, 2015: Fujimoto (2015a)
9. *Halechiniscus yanakaagii* Fujimoto, 2015: Fujimoto (2015a)
10. *Halechiniscus chafarinensis* Grimaldi de Zio and Villora Moreno, 1995: Noda (1998)

Subfamily ORZELISCINAE Schulz, 1963

11. *Orzeliscus belopus* Du Bois-Reymond Marcus, 1952: Suzuki and Kristensen (2014)

Subfamily QUISARCTINAE Fujimoto, 2015

12. *Quisarctus yasumurai* Fujimoto, 2015: Fujimoto (2015b)

Subfamily STYRACONYXINAE Kristensen and Renaud-Mornant, 1983

13. *Angursa clavifera* Noda, 1985 (Fig. 10.1g): Noda (1985, 1994a), Bussau (1992)
14. *Raiarctus aureolatus* Renaud-Mornant, 1981: Suzuki (2010)
15. *Styraconyx nanoqsunguak* Kristensen and Higgins, 1984: Noda (1994a, b)
    Styraconyx sp.: Fujimoto (2015a)
16. *Tholoarctus natans* Kristensen and Renaud-Mornant, 1983: Noda (1994a, b), Suzuki (2010)

Subfamily TANARCTINAE Renaud-Mornant, 1980

17. *Actinarctus* cf. *neretinus* Grimaldi de Zio et al., 1982: Suzuki (2010)
18. *Tanarctus* cf. *hellouetae* Renaud-Mornant, 1984: Suzuki (2010)
19. *Tanarctus diplocerus* Fujimoto et al., 2013: Fujimoto et al. (2013)

Family RENAUDARCTIDAE Kristensen and Higgins, 1984

20. *Renaudarctus psammocryptus* Kristensen and Higgins, 1984: Noda (1994b)

Family STYGARCTIDAE Schulz, 1951
Subfamily STYGARCTINAE De Zio Grimaldi et al., 1992

21. *Neostygarctus lovedeluxe* Fujimoto and Miyazaki, 2013 (Fig. 10.1j): Fujimoto and Miyazaki (2013)
22. *Parastygarctus* cf. *biungulatus* Morone de Lucia et al., 1984: Noda (1993)
23. *Parastygarctus* cf. *mediterranicus* Gallo D'Addabbo et al., 2001: Suzuki (2010)
24. *Parastygarctus sterreri* Renaud-Mornant, 1970: Suzuki (2010)
25. *Parastygarctus higginsi* Renaud-Debyser, 1965: Noda (1994a, b)
26. *Pseudostygarctus mirabilis* De Zio Grimaldi et al., 1998: Suzuki (2010)
27. *Stygarctus ayatori* Fujimoto, 2014: Fujimoto (2014)
28. *Stygarctus spinifer* Hiruta, 1985 (Fig. 10.1h): Hiruta (1985), Gallo d'Addabbo et al. (2001), Hansen et al. (2012)

Order ECHINISCOIDEA Richters, 1926
Family ECHINISCOIDIDAE Krisensen and Hallas, 1980
Anisonyches sp.: Noda (1994b, c), Suzuki (2010)

29. *Echiniscoides sigismundi* (M. Schulze, 1865): Morikawa (1951b)

Family ECHINISCIDAE Thulin, 1928

30. *Cornechiniscus lobatus* (Ramazzotti, 1943): Utsugi (1986, 1987, 1996), Utsugi et al. (1997)
31. *Echiniscus africanus* Murray, 1907: Utsugi (1996)
32. *Echiniscus arctomys* Ehrenberg, 1853: Utsugi (1985a, b)
33. *Echiniscus blumi* Richters, 1903: Mathews (1936–1937)
34. *Echiniscus baius* Marcus, 1928: Utsugi (1987, 1992b, 1996), Utsugi et al. (1997), Ishida and Matsui (2007)
35. *Echiniscus canadensis* Murray, 1910: Ito (1993, 1999), Utsugi (1992b, 1996)
36. *Echiniscus crassispinosus* (Murray, 1907): Utsugi (1996), Ito and Abe (1997)
37. *Echiniscus dreyfusi* De Barros, 1942: Utsugi (1988, 1990, 1992a, 1996), Ishida and Matsui (2007)
38. *Echiniscus elegans* Richters, 1907: Richters (1907), Morikawa (1951a), Utsugi (1992a, 1996), Utsugi et al. (1997), Ito and Abe (1997)
    **Echiniscus fischeri* Richters, 1911: Utsugi (1996), Utsugi et al. (1997), Ishida and Matsui (2007)
39. *Echiniscus hoonsooi* Moon and Kim, 1990: Abe et al. (2000), Abe and Takeda (2000b)
40. **Echiniscus japonicus* Morikawa, 1951 (Fig. 10.1f): Morikawa (1951a), Utsugi (1985a, b, 1986, 1987, 1990a, 1991, 1992b, 1993b, 1994a, 1996), Utsugi et al. (1997), Ishida and Matsui (2007)
41. *Echiniscus kerguelensis* Richters, 1904: Utsugi (1990b, 1994b)
42. *Echiniscus laterospinosus* Rudescu, 1964: Utsugi (1990b, 1994b, 1995)
43. *Echiniscus lapponicus* Thulin, 1911: Mathews (1936–1937), Utsugi (1991, 1993b, 1996)
44. *Echiniscus laterosetosus* Ito, 1993: Ito (1993, 1999), Ishida and Matsui (2007)

45. *Echiniscus limai* Da Cunha and Do Nascimento Ribeiro, 1964: Utsugi (1990b)
46. *Echiniscus merokensis* Richters, 1904: Mathews (1936–1937), Morikawa (1951a), Utsugi (1990b)
47. *Echiniscus* cf. *perviridis* Ramazzotti, 1959: Abe and Takeda (2000b, 2005)
48. *Echiniscus polygonalis* Ito, 1993: Ito (1993, 1999)
49. *Echiniscus quadrispinosus* Richters, 1902: Mathews (1936–1937), Ito (1993, 1999), Ito and Abe (1997)
50. *Echiniscus reticulatus* Murray, 1905: Utsugi et al. (1997), Ishida and Matsui (2007)
51. *Echiniscus rugospinosus* Marcus, 1928: Utsugi (1987, 1996)
52. *Echiniscus semifoveolatus* Ito, 1993: Ito (1993, 1999), Ishida and Matsui (2007)
53. *Echiniscus spiniger* Richters, 1904: Mathews (1936–1937), Utsugi (1990b, 1994b, 1995)
54. *Echiniscus spinulosus* (Doyère, 1840): Mathews (1936–1937), Abe and Kobayashi (2002)
55. *Echiniscus tesselatus* Murray, 1910: Utsugi (1993b, 1996), Ishida and Matsui (2007)
56. *Echiniscus testudo* (Doyère, 1840): (Utsugi, 1987, 1996)
57. *Echiniscus virginicus* Riggin, 1962: Utsugi (1988), Ito (1999)
58. *Echiniscus viridis* Murray, 1910: Utsugi (1996), Ishida and Matsui (2007)
59. *Echiniscus viridissimus* Pterfi, 1956: Utsugi (1994a), Abe and Takeda (2000b)
60. *Hypechiniscus gladiator* (Murray, 1905): Morikawa (1951a), Utsugi (1995)
61. *Pseudechiniscus asper* Abe et al., 1998: Abe et al. (1998)
62. *Pseudechiniscus bartkei* Weglarska, 1962: Utsugi (1996)
63. *Pseudechiniscus facettalis* Petersen, 1951: Ito (1993, 1999), Utsugi (1987, 1992b, 1996), Utsugi et al. (1997), Abe and Kobayashi (2002)
64. *Pseudechiniscus suillus* (Ehrenberg, 1853): Mathews (1936–1937), Utsugi (1987, 1988, 1990b, 1996)
65. *Pseudechiniscus pseudoconifer* Ramazzotti, 1943: Utsugi (1994b, 1995)
66. *Pseudechiniscus ramazzottii* Maucci, 1952: Utsugi (1986, 1987, 1990b)

Class MESOTARIGRADA Rahm, 1937
Order THERMOZODIA Ramazzotti and Maucci, 1983
Family THERMOZODIIDAE Rahm, 1937

67. *Thermozodium esakii* Rahm, 1937: Rahm (1937a, b)

Class EUTARDIGRADA Richters, 1926
Order APOCHELA Schuster et al., 1980
Family MILNESIIDAE Ramazzotti, 1962

68. *Milnesium* cf. *tardigradum* Doyère, 1840 (Fig. 10.1e): Mathews (1936–1937), Hatai (1956, 1959), Utsugi (1985a, b, 1986, 1987, 1988, 1990a, 1991, 1992b, 1994a, b, 1996), Utsugi et al. (1997), Ito (1997, 1999), Ito

and Abe (1997, 2001), Abe and Takeda (2000b), Biserov et al. (2001), Suzuki (2003), Ishimaru (2011)

Order PARACHELA Schuster et al., 1980
Superfamily EOHYPSIBIOIDEA Bertolani and Kristensen, 1987
Family EOHYPSIBIIDAE Bertolani and Kristensen, 1987

69. *Bertolanius weglarskae* (Dastych, 1972): Ito (1991a, 1999), Ito and Abe (1997, 2000)
70. *Eohypsibius terrestris* Ito, 1988: Ito (1988, 1999), Ito and Abe (1997, 2000, 2001)

Superfamily HYPSIBIOIDEA Pilato, 1969
Family CALOHYPSIBIIDAE Pilato, 1969

71. *Calohypsibius ornatus* (Richters, 1900) (Fig. 10.1b): Mathews (1936–1937), Hatai (1959), Utsugi (1993b, 1995), Ito (1991a, 1999), Ito and Abe (1997)

Family HYPSIBIIDAE Pilato, 1969
Subfamily DIPHASCONINAE Datych, 1992

72. *Diphascon alpinum* Muray, 1906: Mathews (1936–1937), Hatai (1956, 1959), Ito (1986), Utsugi (1988)
73. *Diphascon bidropion* Ito, 1995 (Fig. 10.1c): Ito (1995, 1999), Ito and Abe (2001)
74. *Diphascon higginsi* Binda, 1971: Ito and Utsugi (1992), Ito (1995, 1999), Ito and Abe (1997, 2000), Abe and Takeda (2000b), Ishida and Matsui (2007)
75. *Diphascon montigenum* Pilato and Dastych, 1974: Utsugi (1994b), Utsugi et al. (1997)
76. *Diphascon nobilei* (Binda, 1969): Ito (1991b), Ito and Utsugi (1992), Utsugi (1996), Utsugi et al. (1997), Ito and Abe (2000), Harada and Ito (2006)
77. *Diphascon patanei* (Binda and Pilato, 1971): Ito (1991b), Ito and Utsugi (1992)
78. *Diphascon pingue* (Marcus, 1936): Ito and Utsugi (1992), Utsugi (1994b, 1995, 1996), Ito (1995, 1999), Ito and Abe (1997, 2000), Harada and Ito (2006), Ishida and Matsui (2007)
79. *Diphascon rugosum* (Bartos, 1935): Ito (1991b), Ito and Utsugi (1992), Ito and Abe (1997)
80. *Diphascon tenue* Thulin, 1928: Ito and Abe (2000)
81. *Diphascon mariae* (Mihelcic, 1949): Ito and Utsugi (1992), Utsugi (1995)
82. *Diphascon trachydorsatum* (Bartos, 1937): Utsugi (1995)

Subfamily HYPSIBIINAE Pilato, 1969

83. **Hypsibius choucoutiensis* Rahm, 1937: Rahm (1937a, b, c)
84. *Hypsibius convergens* (Uranowicz, 1925): Utsugi (1996), Utsugi et al. (1997), Ito (1999), Biserov et al. (2001), Ishida and Matsui (2007)

85. *Hypsibius dujardini* (Doyère, 1840): Utsugi (1986, 1996), Utsugi et al. (1987), Abe and Takeda (2000b, 2005), Biserov et al. (2001), Ito (1999), Ishida and Matsui (2007)
86. *Hypsibius giusepperamazzotti* Sudzuki, 1975: Sudzuki (1975)
87. *Hypsibius maculatus* Iharos, 1969: Utsugi (1988, 1993b)
88. *Hypsibius microps* Thulin, 1928: Utsugi (1996), Utsugi et al. (1997), Ishida and Matsui (2007)
89. *Hypsibius morikawai* Ito, 1995: Ito (1995, 1999)
90. *Hypsibius runae* Bartos, 1941: Utsugi (1995)
91. *Hypsibius* cf. *scabropygus* Cuénot, 1929: Ito (1999), Ito and Abe (1997)

Subfamily ITAQUASCONINDAE Barto in Rudescu, 1964

92. *Adropion arduifrons* (Thulin, 1928): Ito and Abe (1997)
93. *Adropion belgicae* (Richters, 1911): Ito (1986, 1995, 1999), Ito and Utsugi (1992), Ito and Abe (2000)
    =*Fujiscon diphasconiellum* Ito, 1991: Ito (1991a)
94. *Adropion calorae* (Binda and Pilato, 1969): Ito (1986, 1995, 1999), Ito and Utsugi (1992)
95. *Adropion montigenum* (Pilato and Dastych, 1974): Ito and Abe (2001)
96. *Adropion prorsirostre* (Thulin, 1928): Ito and Utsugi (1992), Ito (1995, 1999), Utsugi et al. (1997), Ito and Abe (2000, 2001)
97. *Adropion scoticum* (Murray, 1905): Ito (1986, 1995, 1999), Ito and Utsugi (1992), Utsugi (1992a, 1987), Ito and Abe (1997, 2000, 2001), Ishida and Matsui (2007)
98. *Astatumen tamaensis* (Sudzuki, 1975): Sudzuki (1975)
99. *Astatumen trinacriae* (Arcidiacono, 1962): Ito (1991b), Ito and Abe (2000)
100. *Itaquascon* cf. *mongolicum* Kaczmarek et al., 2002: Harada and Ito (2006)
101. *Itaquascon globuliferum* Abe and Ito, 1994: Abe and Ito (1994), Ito and Abe (2000, 2001)
102. *Itaquascon pawlowskii* Weglarska, 1973: Ito (1995, 1999), Abe and Takeda (2000b)
103. *Itaquascon umbellinae* de Barros, 1939: Ito (1995, 1999), Ito and Abe (1997, 2000, 2001), Harada and Ito (2006), Ishida and Matsui (2007)
104. *Mesocrista spitzbergense* (Richters, 1903): Utsugi (1986), Ito (1986, 1995, 1999), Ito and Abe (2001)
105. *Platicrista affine* (Mihelcic, 1951): Utsugi (1996)
106. *Platicrista angustata* (Murray, 1905): Ito (1986, 1995, 1999), Utsugi et al. (1997), Ito and Abe (2001), Ishida and Matsui (2007)

Subfamily PILATOBIINAE Bertolani et al., 2014

107. *Pilatobius brevipes* (Marcus, 1936): Harada and Ito (2006)
108. *Pilatobius bullatus* (Murray, 1905): Ito and Abe (1997)
109. *Pilatobius oculatus* (Murray, 1906): Ito (1986, 1995, 1999), Ito and Utsugi (1992), Ito and Abe (2000)

110. *Pilatobius patanei* (Binda and Pilato, 1971): Ito and Utsugi (1992), Harada and Ito (2006)
111. *Pilatobius recamieri* (Richters, 1911): Ito and Utsugi (1992), Utsugi (1995), Utsugi et al. (1997)
112. *Pilatobius rugosus* (Bartos, 1935): Ito and Utsugi (1992), Ito and Abe (1997)
113. *Pilatobius sexbullatus* (Ito, 1995): Ito (1995, 1999)

Family MICROHYPSIBIIDAE Pilato, 1998

114. *Microhypsibius japonicus* Ito, 1991 (Fig. 10.1a): Ito (1991a, 1999)
115. *Microhypsibius truncatus* Thulin, 1928: Ito and Abe (1997, 2000)

Family RAMAZZOTTIIDAE Sands et al., 2008

116. *Ramazzottius baumanni* (Ramazzotti, 1962): Utsugi (1988, 1991, 1992b, 1996), Utsugi et al. (1997), Ito and Abe (1997), Ishida and Matsui (2007)
117. *Ramazzottius cataphractus* (Maucci, 1974): Utsugi (1995), Utsugi et al. (1997)
118. *Ramazzottius novemcinctus* (Marcus, 1936): Utsugi (1988, 1994a, 1996), Utsugi et al. (1997), Ishida and Matsui (2007)
119. *Ramazzottius oberhaeuseri* (Doyère, 1840): Mathews (1936–1937), Hatai (1959), Utsugi (1985a, b, 1994a, 1996), Utsugi et al. (1997), Ito (1995, 1999)
120. *Ramazzottius varieornatus* Bertolani and Kinchin, 1993: Horikawa et al. (2008)

Superfamily ISOHYPSIBIOIDEA Sands et al., 2008
Family ISOHYPSIBIIDAE Sands et al., 2008

121. *Doryphoribius dupliglobulatus* Ito, 1995: Ito (1995, 1999), Ito and Abe (1997, 2000)
122. *Isohypsibius basalovoi* (Duarnte Pasa and Maucci, 1972): Utsugi (1994b, 1995)
123. *Isohypsibius cameruni* (Iharos, 1969): Ito (1995, 1999), Harada and Ito (2006)
124. *Isohypsibius canadensis* (Murray, 1910): Hatai (1956, 1959), Utsugi (1985a, b, 1994a, b), Utsugi et al. (1997)
125. *Isohypsibius eplenyensis* (Iharos, 1970): Utsugi (1988, 1996)
126. *Isohypsibius* aff. *granulifer* Thulin, 1928: Biserov et al. (2001)
127. *Isohypsibius hydrogogianus* Ito and Tagami, 1993: Ito and Tagami (1993)
128. *Isohypsibius latiunguis* (Iharos, 1964): Harada and Ito (2006)
129. *Isohypsibius lunulatus* (Iharos, 1966): Utsugi et al. (1997)
130. *Isohypsibius mammillosus* (Iharos, 1964): Ishida and Matsui (2007)
131. *Isohypsibius marcellinoi* Binda and Pilato, 1971: Harada and Ito (2006)
132. *Isohypsibius myrops* (du Bois-Reymond Marcus, 1944): Utsugi (2005)
133. *Isohypsibius nipponicus* Sudzuki, 1975: Sudzuki (1975)
134. *Isohypsibius novaeguineae* (Iharos, 1967): Utsugi (1999)

135. *Isohypsibius prosotomus* Thulin, 1928: Biserov et al. (2001)
136. *Isohypsibius reticulatus* Pilato, 1973: Utsugi (1992b, 1996), Abe and Takeda (2000b)
137. *Isohypsibius ronsisvallei* (Binda and Pilato, 1969): Ito (1991b), Harada and Ito (2006)
138. *Isohypsibius sattleri* (Richters, 1902): Utsugi et al. (1997)
139. *Isohypsibius schaudinni* (Richters, 1909): Hatai (1956, 1959), Utsugi (1987, 1992b, 1993b, 1994a, 1996)
140. *Isohypsibius tetradactyloides* (Richters, 1907): Biserov et al. (2001)
141. *Isohypsibius theresiae* (Iharos, 1964): Ito (1991b)
142. *Pseudobiotus spinifer* Chang et al., 2007: Fujimoto and Miyazaki (2011)
143. *Pseudobiotus vladimiri* Biserov et al., 2001: Biserov et al. (2001)
144. *Thulinius augusti* (Murray, 1907): Morikawa (1967)
145. *Thulinius itoi* (Tsurusaki, 1980): Tsurusaki (1980), Kaczmarek and Michalczyk (2006)
146. *Thulinius sartursus* (Schuster et al., 1978): Biserov et al. (2001)

Superfamily MACROBIOTOIDEA Thulin, 1928 in Marley et al. 2011

147. *Adorybiotus granulatus* (Richters, 1903): Utsugi (1992a), Ito (1997, 1999), Ito and Abe (2000)
148. *Calcarobiotus imperialis* Abe and Takeda, 2000 (Fig. 10.1d): Abe and Takeda (2000a, b)
149. *Insuetifurca austronipponica* Abe, 2005: Abe (2005)
150. *Insuetifurca fujiensis* (Ito, 1997): Ito (1997, 1999)
151. *Macrobiotus crenulatus* Richters, 1904: [=*M. dentatus*] Utsugi et al. (1997), Ito (1997, 1999)
152. *Macrobiotus echinogenitus* Richters, 1903: Mathews (1936–1937), Utsugi (1986, 1988)
153. *Macrobiotus grandis* Richters, 1911: Hatai (1956), Utsugi (1995)
154. *Macrobiotus harmsworthi* Murray, 1907: Mathews (1936–1937), Utsugi (1985a, b, 1986, 1987, 1988, 1991, 1992b, 1993b, 1994a, b, 1996), Utsugi et al. (1997), Biserov et al. (2001), Ishida and Matsui (2007)
155. *Macrobiotus hufelandi* Schultze, 1834: Mathews (1936–1937), Hatai (1956), Utsugi (1985a, b, 1986, 1987, 1988, 1990a, 1991, 1992b, 1993b, 1994a, b, 1996), Ito (1997), Utsugi et al. (1997), Biserov et al. (2001)
156. *Macrobiotus mauccii* Pilato, 1974: Utsugi (1988), Abe and Takeda (2000b, 2005)
157. *Macrobiotus occidentalis* Murray, 1910: Mathews (1936–1937), Hatai (1956), Utsugi (1986, 1987, 1996), Biserov et al. (2001), Ishida and Matsui (2007)
158. *Macrobiotus orcadensis* Murray, 1907: Utsugi (1993a), Ito (1997, 1999)
159. *Macrobiotus topali* Iharos, 1969: Utsugi (1996), Ishida and Matsui (2007)
160. *Minibiotus hufelandioides* (Murray, 1910): Utsugi (1985a, b, 1986, 1992b, 1994a)

161. *Minibiotus intermedius* (Plate, 1888): Utsugi (1985a, b, 1986, 1987, 1988, 1990a, 1992b, 1993b, 1994a, b, 1996), Utsugi et al. (1997), Ito (1997, 1999), Ito and Abe (2000, 2001), Abe and Takeda (2005)
162. *Paramacrobiotus areolatus* (Murray, 1907): Mathews (1936–1937), Hatai (1959)
163. *Paramacrobiotus richtersi* (Murray, 1911): Utsugi (1986, 1996), Ito (1997, 1999), Ito and Abe (1997, 2000), Utsugi et al. (1997), Ishida and Matsui (2007)

Family MURRAYIDAE Guidetti et al., 2000

164. *Dactylobiotus ampullaceus* (Thulin, 1911): Sudzuki (1975)
165. *Dactylobiotus dispar* (Murray, 1907): Biserov et al. (2001), Fujimoto and Miyazaki (2011)
166. *Dactylobiotus macronyx* (Dujardin, 1851): Kawamura (1918)
167. *Murrayon hibernicus* (Murray, 1911): Utsugi (1996), Ito (1997, 1999), Ito and Abe (1997, 2000), Utsugi et al. (1997), Ishida and Matsui (2007)

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References

Abe W (2005) *Insuetifurca austronipponica*, a new tardigrade (Eutardigrada: Macrobiotidae) from Kagoshima, southern Japan. Zool Sci 22:1295–1299

Abe W, Ito M (1994) *Itaquascon globuliferum*, a new species of Tardigrada (Eutardigrada: Hypsibiidae) from Japan. Proc Jap Soc Syst Zool 51:8–11

Abe W, Kobayashi N (2002) Phylogeny of tardigrades (water bears) inferred from 28S rDNA sequences. Zool Sci 19:1142

Abe W, Takeda M (2000a) A new *Calcarobiotus* (Tardigrada: Macrobiotidae) from the Imperial Palace of Japan. Zool Sci 17:259–263

Abe W, Takeda M (2000b) Tardigrades from the Imperial Palace, Tokyo. Mem Natl Sci Mus Tokyo 35:165–177

Abe W, Takeda M (2005) Semiterrestrial tardigrades from the Tokiwamatsu Imperial Villa, Tokyo, Japan. Mem Natl Sci Mus Tokyo 39:503–510

Abe W, Utsugi K, Takeda M (1998) *Pseudechiniscus asper*, a new Tardigrada (Heterotardigrada: Echiniscidae) from Hokkaido, northern Japan. Proc Biol Soc Wash 111:843–848

Abe W, Ito M, Takeda M (2000) First record of *Echiniscus hoonsooi* (Tardigrada: Echiniscidae) from Japan. Species Divers 5:103–110

Abukawa S (2010) Hokkaido engan-iki no kaisan kumamushi 4 shu [Four species of marine tardigrades in the coastal area around Hokkaido]. Umiushi-Tsushin 69:8–9 [in Japanese]

Biserov VI, Dudichev AL, Biserova NM (2001) Preliminary data on tardigrades of Lake Biwa (Japan). Arthropoda Sel 10:307–310

Bussau C (1992) New deep-sea Tardigrada (Arthrotardigrada, Halechiniscidae) from a manganese nodule area of the eastern South Pacific. Zool Scr 21:79–91

Degma P, Guidetti R (2007) Notes to the current checklist of Tardigrada. Zootaxa 1579:41–53

Degma P, Bertolai R, Guidetti R (2015) Actual checklist of Tardigrada species. (2009–2015, Ver. 28: 31-03-2015) http://www-tardigrada.modena.unimo.it/miscellanea/Actual%20checklist%20of%20Tardigrada.pdf. Accessed 15 Nov 2015

Doyère LMF (1840) Mémoire sur les tardigraes. Ann Sci Nat Sér 2(14):269–361

Esaki T (1930) Myriapoda and Arachnida [in Japanese]. In: Iwanami Koza Biology, Zoology. Iwanami Shoten, Tokyo, p 128

Fujimoto S (2014) A new *Stygarctus* (Arthrotardigrada: Stygarctidae) from Japan, with entangled seminal receptacle ducts. Zootaxa 3784:187–195

Fujimoto S (2015a) Halechiniscidae (Heterotardigrada, Arthrotardigrada) of Oura Bay, Okinawajima, Ryukyu Islands, with descriptions of three new species. ZooKeys 483:149–166

Fujimoto S (2015b) *Quisarctus yasumurai* gen. et sp. nov. (Arthrotardigrada: Halechiniscidae) from a submarine cave, off Iejima, Ryukyu Islands, Japan. Zootaxa 3948:145–150

Fujimoto S, Miyazaki K (2011) Preliminary notes on the freshwater tardigrades from the Kamo River, Kyoto. Proc Arthropod Embryol Soc Jpn 46:39–40

Fujimoto S, Miyazaki K (2013) *Neostygarctus lovedeluxe* n. sp. from the Miyako Islands, Japan: the first record of Neostygarctidae (Heterotardigrada: Arthrotardigrada) from the Pacific. Zool Sci 30:414–419

Fujimoto S, Miyazaki K, Suzuki AC (2013) A new marine tardigrade, *Tanarctus diplocerus* (Arthrotardigrada: Halechiniscidae) from Japan. J Mar Biol Assoc UK 93:955–961

Gallo D'Addabbo M, De Zio Grimaldi S, Sandulli R (2001) Heterotardigrada of two submarine caves in S. Domino Island (Tremiti Islands) in the Mediterranean Sea with the description of two new species of Stygarctidae. Zool Anz 240:361–369

Goeze (1773) Über den kleinen Wasserbär. In: Herrn Karl Bonnet's Abhandlungen aus der Insektologie, JJ Gebauers Wittwe und Joh Jac Gebauer, Halle, pp 367–375

Guidetti R, Bertolani R (2005) Tardigrada taxonomy: an updated checklist of the taxa and a list of characters for their identification. Zootaxa 845:1–46

Hansen JG, Kristensen RM, Jørgensen A (2012) The armoured marine tardigrades (Arthrotardigrada, Tardigrada). Sci Dan Ser B Biol 2

Harada H, Ito M (2006) Soil-inhabiting tardigrade communities in forests of Central Japan. Hydrobiologia 558:119–127

Hatai S (1956) On the Japanese Tardigrada. Sci Rep Yokosuka City Mus 1:1–13

Hatai S (1959) The distribution of *Milnesium tardigradum* Doy. in Japan. Sci Rep Yokosuka City Mus 4:5–12 [in Japanese with English abstract]

Hiruta S (1985) A new species of marine interstitial Tardigrada of the genus *Stygarctus* Schulz from Hokkaido, Japan. Spec Publ Mukaishima Mar Biol Stn 245:127–129

Horikawa DD, Kunieda T, Abe W, Watanabe M, Nakahara Y, Yukuhiro F, Sakashita T, Hamada N, Wada S, Funayama T, Katagiri C, Kobayashgi Y, Higashi S, Okuda T (2008) Establishment of a rearing system of the extremotolerant tardigrade *Ramazzottius varieornatus*: a new model animal for astrobiology. Astrobiology 8:549–556

Horikawa DD, Yamaguchi A, Sakashita T, Tanaka D, Hamada N, Yukuhiro F, Kuwahara H, Kunieda T, Watanabe M, Nakahara Y, Wada S, Funayama T, Katagiri C, Higashi S, Yokobori S, Kuwabara M, Rothschild LJ, Okuda T, Hashimoto H, Kobayashi Y (2012) Tolerance of anhydrobiotic eggs of the tardigrade *Ramazzottius varieornatus* to extreme environments. Astrobiology 12:283–289

Horikawa DD, Cumbers J, Sakakibara I, Rogoff D, Leuko S, Harnoto R, Arakawa K, Katayama T, Kunieda T, Toyoda A, Fujiyama A, Rothschild LJ (2013) Analysis of DNA repair and protection in the tardigrade *Ramazzottius varieornatus* and *Hypsibius dujardini* after exposure to UVC radiation. PLoS One 8(6):e64793. doi:10.1371/journal.pone.0064793

Iijima I (1889) A textbook of zoology. Keigyo-sha, Tokyo [in Japanese]

Iijima I (1918) A manual of zoology. Dainippon Tosho, Tokyo [in Japanese]

Ishida M, Matsui T (2007) Noteworthy tardigrades from Kochi Prefecture. Nat Environ Sci Res 9:45–58

Ishimaru S (2011) Records of three species of Tardigrada from Ishikawa Prefecture, Japan. Bull Ishikawa Mus Nat His 1:45–47

Ito M (1986) Genus *Diphascon* (Eutardigrada: Hypsibiiae) from Mt. Fuji, Central Japan. Zool Sci 3:1110

Ito M (1988) A new species of the genus *Eohypsibius* (Eutardigrada: Eohypsibiidae) from Japan. Edaphologia 39:11–15

Ito M (1991a) Taxonoic study on the Eutaridigrada from the northern slope of Mt. Fuji, central Japan. Proc Jap Soc Syst Zool 45:30–43

Ito M (1991b) Terrestrial tardigrade fauna of the Tokyo University forest in Chiba. Zool Sci 8:1198

Ito M (1993) Taxonomic study on the class Heterotardigrada (Tardigrada) from the northern slope of Mt. Fuji, central Japan. Edaphologia 50:1–13

Ito M (1995) Taxonomic study on the Eutardigrada from the northern slope of Mt. Fuji, central Japan, II. Family Hypsibiidae. Proc Jap Soc Syst Zool 53:18–39

Ito M (1997) Taxonomic study on the Eutardigrada from the northern slope of Mt. Fuji, central Japan. III. Families Macrobiotidae and Milnesiidae. Species Divers 2:167–178

Ito M (1999) Ecological distribution, abundance and habitat preference of terrestrial tardigrades in various forests on the northern slope of Mt. Fuji, central Japan. Zool Anz 238:225–234

Ito M, Abe W (1997) Tanzawa sanchi no rikusei kumamushi rui [Terrestrial tardigrades in the Tanzawa Mountains]. In: Kanagawa Park Association, Tanzawa Ōyama Natural Environment Census Committee (eds) Report of Tanzawa Ōyama Natural Environment Census. Department of Environment, Kanagawa Prefectural Government, Yokohama, pp 283–284, 329–330 [in Japanese]

Ito M, Abe W (2000) Odamiyama no rikusei kumamushi rui [Terrestrial tardigrades in Odamiyama]. In: Yamamoto Shinrin Seibutsu Kenkyujo et al. (eds) Odamiyama no shizen, vol 1 [Nature in Odamiyama, vol 1]. Odamachi, Oda, pp 649–662 [in Japanese]

Ito M, Abe W (2001) Micro-distribution of soil-inhabiting tardigrades (Tardigrada) in a sub-alpine coniferous forest of Japan. Zool Anz 240:403–407

Ito M, Tagami K (1993) A new species of the genus *Isohypsibius* (Eutardigrada: Hypsibiidae) collected from municipal water supply in Japan. Jpn J Limnol 54:81–83

Ito M, Utsugi K (1992) Genus *Diphascon* (Tardigrada) from Japan. Zool Sci 9:1297

Kaczmarek Ł, Michalczyk Ł (2006) *Thulinius itoi* comb. nov. a new systematic position for *Isohypsibius itoi* (Tsurusaki, 1980) (Tardigrada: Eutardigrada: Hypsibiidae). Zootaxa 1373:65–68

Kagoshima H, Imura S, Suzuki AC (2013) Molecular and morphological analysis of an Antarctic tardigrade, *Acutuncus antarcticus*. J Limnol 72(s1):15–23

Kawamura T (1918) Nihon tansui seibutsugaku, jō kan [Japanese freshwater biology, vol I]. Shōkabō, Tokyo [in Japanese]

Kishida K (1910) Kumamushi ni tsuite [On tardigrades]. Hakubutsu no tomo 10:160–164 [in Japanese]

Kishida K (1927) Tardigrades. In: Uchida S (ed) Illustrated encyclopedia of animals in Japan. Hokuryūkan, Tokyo, p 988 [in Japanese]

Kume A, Suzuki AC, Tojo K (2012) A study into the dispersion pattern of *Milnesium* cf. *tardigradum*: a molecular phylogenetic approach. In: Abstracts of the 12th international symposium on Tardigrada, Vila Nova de Gaia, Portugal, 23–26 July 2012, p 77

Marcus E (1929) Tardigrada. Bronn's Klassen und Ordnungen des Tierreichs, Bd 5, IV-3. Akademische Verlagsgesellschaft, Leipzig

Mathews G (1936–1937) Tardigrada from Japan. Peking Nat Hist Bull 11:411–412

Morikawa K (1951a) Notes on four interesting *Echiniscus* (Tardigrada) from Japan. Annot Zool Jpn 24:108–110

Morikawa K (1951b) Kaisei kumamushi no saishū [Notes on a marine water-bear (Tardigrada)]. Saishū to shiiku 13:170–172 [in Japanese]

Morikawa K (1957) Kanporui (Tardigrada) no bunrui to keitou [Taxonomy and phylogeny of tardigrades]. Atypus 12:3–11 [in Japanese]

Morikawa K (1967) Tardigrada. In: Uchida T, Yamada M, Yamaguchi H, Nagao Z, Kato K, Morikawa K (eds) Systematic zoology, vol 6. Nakayama-Shoten, Tokyo, pp 295–333 [in Japanese]

Noda H (1985) Description of a new subspecies of *Angursa biscupis* Pollock (Heterotardigrada, Halechiniscidae) from Tanabe Bay, Japan. Publ Seto Mar Biol Lab 30:269–276

Noda H (1987) A new species of marine Tardigrada of the genus *Florarctus* (Heterotardigrada, Halechiniscidae) from Japan. Publ Seto Mar Biol Lab 32:323–328

Noda H (1989) The first occurrence of coronarctid tardigrade from the shallow water. Zool Sci 6:1220

Noda H (1993) Stygarctid tardigrade showing neoteny from Kuroshima Island, Ryukyu Archipelago. Zool Sci 10(Suppl):175

Noda H (1994a) Tardigrades from sand beaches in Okinawa. Proc Jap Soc Syst Zool 51:79 [in Japanese]

Noda H (1994b) Two renaudarctids (Arthrotardigrada) from Ryukyu Archipelago, Japan. In: Abstracts of the 6th International Symposium on Tardigrada, Selwyn College, Cambridge, 22–26 August 1994. http://www.tardigrada.net/newsletter/symposia_06.htm#Proceedings. Accessed 16 Jan 2016

Noda H (1994c) An undescribed *Anisonyches* sp. (Tardigrada) with a large basal spur on the external claw from Ryukyu Islands. Zool Sci 11(Suppl):33

Noda H (1998) Two halechiniscid tardigrades from Japan and a similarity in marine tardigrade fauna between Japan and the Mediterranean. Zool Sci 15(Suppl):37

Nonogaki H, Gamô S (1989) Note on the distribution of some terrestrial tardigrades or water-bears in the coastal region of Kanagawa Prefecture. Rep Manazuru Mar Lab Sci Educ 5:27–34 [in Japanese with English summary]

Okamura K (1908) Shô-tenchi. Hakubutsugaku Zasshi 9(98):1–6 [in Japanese]

Rahm G (1937a) Tardigraden vom Yan-Chia-Ping-Tal (Nordchina). Zool Anz 119:105–111

Rahm G (1937b) A new order of tardigrades from the hot springs of Japan (Furu-yu section, Unzen). Annot Zool Jpn 16:345–352

Rahm G (1937c) Eine neue Tardgraden-ordnung aus den heissen Quellen von Unzen, Insel Kyushu, Japan. Zool Anz 121:65–71

Ramazzotti G (1962) Il Phylum Tardigrada. Mem Ist Ital Idrobiol 14:1–595

Ramazzotti G, Maucci W (1983) Il Phylum Tardigrada, 3rd edn. Mem Ist Ital Idrobiol 41:1–1012

Richters F (1907) Zwei neue Echiniscus-Arten. Zool Anz 31:197–202

Saikawa M, Oyama M (1992) Electron microscopy on infection of tardigrades by *Ballocephala spaerospora* and *B. verrucospora* conidia. Trans Mycol Soc Jpn 33:305–311

Saikawa M, Oyama M, Yamaguchi K (1991) *Harposporium anguillulae* and *Haptoglossa intermedia* parasitizing tardigrades. Trans Mycol Soc Jpn 32:501–508

Spallanzani (1776) Opuscoli di fisica animale, e vegetabile, vol 2, Modena

Sudzuki M (1975) Lotic Tardigrada from the Tama River with special reference to water saprobity. Mem Ist Ital Idrobiol Pallanza 32(Suppl):377–391

Sudzuki M (1979) Some aspects of the haline interstitial biota from Ryukyu Shoto, subtropical chain islands, Southwest Japan. Sesoko Mar Sci Lab Tech Rep 6:37–49, plates I–IV

Suzuki AC (2003) Life history of *Milnesium tardigradum* Doyère (Tardigrada) under a rearing environment. Zool Sci 20:49–57

Suzuki AC (2006) Kumamushi–Chîsana Kaibutsu [in Japanese] (Tardigrades–the Little Monster). Iwanami Shoten, Tokyo

Suzuki AC (2008) Appearance of males in a thelytokous strain of *Milnesium* cf. *tardigradum* (Eutardigrada: Apochela). Zool Sci 25:849–853

Suzuki AC (2010) Tardigrades of Japanese coast: water bears of Shimabara Bay [in Japanese]. Umiushi-Tsūshin 67:2–3

Suzuki AC, Kristensen RM (2014) Spermatozoa in the reproductive system of a hermaphroditic marine tardigrade, *Orzeliscus belopus* (Tardigrada: Arthrotardigrada). Zool Anz 253:497–511

Suzuki AC, Moriyama K (2008) Kumamusi wo kau niwa [in Japanese] (What if You Rear Water Bear). Chijin Shokan, Tokyo

Tanaka S, Tanaka J, Niwa Y, Horikawa DD, Katayama T, Arakawa K, Toyoda A, Kubo T, Kunieda T (2015) Novel mitochondria-targeted heat-soluble proteins identified in the anhydrobiotic tardigrade improve osmotic tolerance of human cells. PLoS One 10(2): e0118272. doi:10.1371/journal.pone.0118272

Tsujimoto M, Suzuki AC, Imura S (2015) Life history of the Antarctic tardigrade, *Acutuncus antarcticus*, under a constant laboratory environment. Polar Biol 38:1575–1581

Tsujimoto M, Imura S, Kanda H (2016) Recovery and reproduction of an Antarctic tardigrade retrieved from a moss sample frozen for over 30 years. Cryobiology 72:78–81

Tsurusaki N (1980) A new species of marine interstitial tardigrada of the genus *Hypsibius* from Hokkaido, Northern Japan. Ann Zool Jpn 53:280–284

Utsugi K (1985a) Rikusei no kumamushi rui [Terrestrial tardigrades]. Iden 9(11):42–51 [in Japanese]

Utsugi K (1985b) Urban tardigrades in Tokyo. Zool Sci 2:1006

Utsugi K (1986) Urban tardigrades in Kyushu. Zool Sci 3:1110

Utsugi K (1987) Urban tardigrades in Hokuriku area. Zool Sci 4:1111

Utsugi K (1988) Tardigrades in Hokkaido area. Zool Sci 5:1335

Utsugi K (1990a) Tardigrades in the 23 wards of Tokyo. Proc Jap Soc Syst Zool 41:71–72

Utsugi K (1990b) Heterotardigrades in Japan. Zool Sci 7:1183

Utsugi K (1991) Tardigrades in Kei-Hanshin area. Proc Jap Soc Syst Zool 45:71

Utsugi K (1992a) Mountain tardigrades in Tokyo. Proc Jap Soc Syst Zool 47:69

Utsugi K (1992b) Urban tardigrades in the Tohoku area. Zool Sci 9:1297

Utsugi K (1993a) Mountain tardigrades in neighboring prefectures around Tokyo. Proc Jap Soc Syst Zool 49:61–62

Utsugi K (1993b) Terrestrial tardigrades in the Ryukyu area. Zool Sci 10(suppl):174

Utsugi K (1994a) Study on terrestrial tardigrades in Japan. I. Urban areas in Kanto region. Nat Environ Sci Res 7:29–34 [in Japanese with English abstract]

Utsugi K (1994b) Mountain tardigrades in Tokyo II. Proc Jap Soc Syst Zool 51:78–79

Utsugi K (1995) Terrestrial tardigrades from mountain areas of Japan. Zool Sci 12(suppl):36

Utsugi K (1996) Study on terrestrial tardigrades in Japan. II. Summary of urban tardigrades in Japan. Nat Environ Sci Res 9:33–46 [in Japanese with English abstract]

Utsugi K (1999) Tardigrada. In: Aoki J (ed) Pictorial keys to soil animals of Japan. Tokai University Press, Tokyo, pp 111–132 [in Japanese]

Utsugi K (2005) Tardigrade living in sewage treatment plants. Nat Environ Sci Res 18:1–8 [in Japanese with English abstract]

Utsugi K, Hiraoka T, Nunomura N (1997) On the relation between tardigrade fauna and bryophyte flora in Toyama Prefecture. Bull Toyama Sci Mus 20:57–71 [in Japanese with English abstract]

Watanabe Y, Sasaki K, Taira K (1961) Preliminary survey of tardigrades on dead bamboo-leaves from Chiba Prefecture. Sci Rep Yokosuka City Mus 6:93–96

Yamaguchi A, Tanaka S, Yamaguchi S, Kuwahara H, Takamura C, Imajoh-Ohmi S, Horikawa DD, Toyoda A, Katayama T, Arakawa K, Fujiyama A, Kubo T, Kunieda T (2012) Two novel heat-soluble protein families abundantly expressed in an anhydrobiotic tardigrade. PLoS One 7 (8):e44209. doi:10.1371/journal.pone.0044209

Chapter 11
Current Status of Entomophilic Nematode Survey in Japan

Natsumi Kanzaki

Abstract The phylum Nematoda, a group of microscopic roundworms, is one of the most divergent and abundant groups of animals. However, their biological diversity and species richness have not been understood sufficiently. Because all nematodes are semiaquatic animals requiring moisture for propagation, they often use other animals, especially insects, as a host and carrier, in terrestrial environments. These insect-associated forms are generally termed 'entomophilic nematodes.' In this present chapter, the diversity of biological features of the entomophilic nematodes found in the Japanese Islands is introduced and compared with previous studies conducted in American and European regions.

Keywords Insect association • Nematode • Parasitism • Pathogenicity • Phoresy • Taxonomy

> In short, if all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes. The location of towns would be decipherable, because for every massing of human beings there would be a corresponding massing of certain nematodes. Trees would still stand in ghostly rows representing our streets and highways. The location of the various plants and animals would still be decipherable, and, had we sufficient knowledge, in many cases even their species could be determined by an examination of their erstwhile nematode parasites. Cobb, N.A. (1914)

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11.1 Introduction

Nematodes, microscopic invertebrates belonging to the phylum Nematoda, are a significantly divergent group. However, their diversity has not been sufficiently explored so far, and even the hypothesized number of species varies among researchers.

In this chapter, the taxonomic and diversity issues of insect-associated nematodes in the Japan Islands are introduced, comparing the studies conducted in other areas.

11.2 General Features of Nematodes

11.2.1 Taxonomic Status of the Phylum Nematoda

The phylum Nematoda is defined by its possession of (1) a bilaterally symmetrical, thread-like or worm-like body without segmentation; (2) a complete digestive system, that is, stoma, pharynx, intestine, rectum, and anus; (3) a pseudocoel; (4) spiral, unequal, determinate cleavage; and (5) longitudinal muscle without circular muscle. However, because of many exceptions in its body shape [e.g., mature females of several agricultural pest species (root-knot nematodes and cyst nematodes) have spherical bodies, and several marine species have segment-like body-surface sculpturing], and difficulties in the observation of the ultrastructure and developmental pattern, it would be more practical to define the phylum based on a molecular phylogenetic context.

Phylogenetically, the phylum belongs to an infrakingdom (or superphylum), Ecdysozoa, which contains Arthropoda (arthropods), Onychophora, Tardigrada (waterbears), Kinorhyncha, Priapulida, Loricifera, Nematomorpha (horsehair worms), and Nematoda. Within these phyla, Nematoda is the sister clade of Nematomorpha (Zrzavý et al. 1998).

11.2.2 Taxonomic Framework of Nematoda

As with the other metazoan organisms, nematodes were traditionally classified according to morphological characters, and the taxonomic system proposed by Inglis (1983) and Maggenti (1983, 1991) was integrated and had been widely accepted. In the traditional system, the phylum was separated into two classes according to the presence or absence of phasmids and caudal glands, the secretory-excretory system at the tail region, and then separated into five subclasses (20 orders) according to feeding and digestive structures. Contrastingly, Blaxter et al. (1998) conducted a molecular phylogenetic analysis of wide-ranging

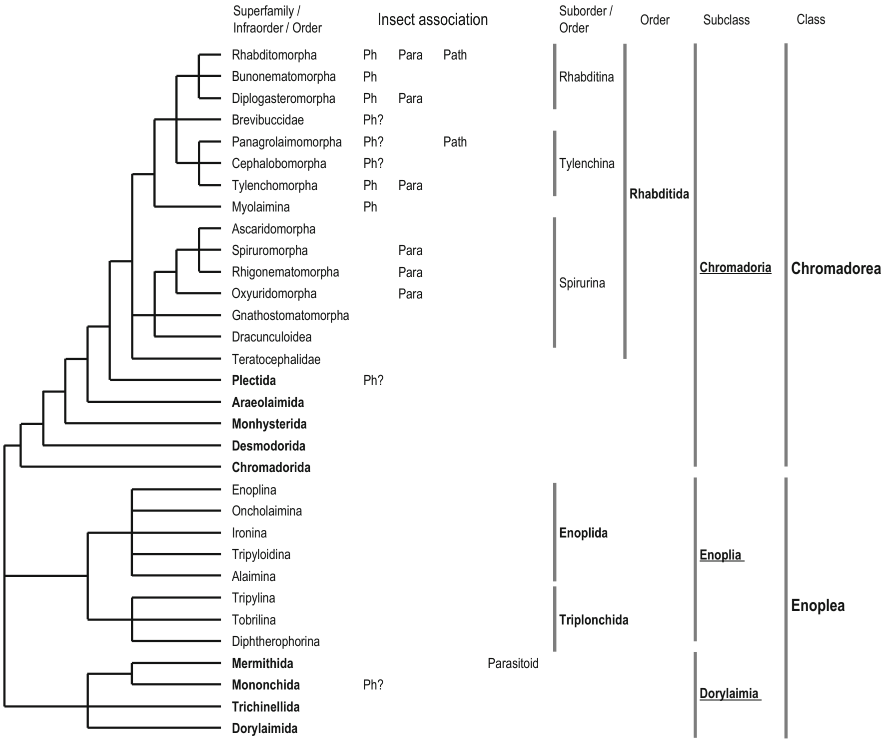


Fig. 11.1 Phylogenetic relationship among orders, suborders, infraorders, and superfamilies of nematodes. Orders, subclasses, and classes are suggested in *bold*, *bold + underline*, and *bold larger character*, respectively. The insect association in each taxonomic group, i.e., phoretic (*Ph*), parasitic (*Para*), pathogenic (*Path*), and parasitoid (*Parasitoid*), are suggested on the right of each taxonomic group, if the associations have been reported. (Modified after De Ley and Blaxter 2002)

nematodes based on small subunit ribosomal RNA gene sequences, and further, De Ley and Blaxter (2002) proposed a new taxonomic framework of the phylum based on their molecular phylogenetic analysis. This new taxonomic system has been updated several times (Holterman et al. 2006; Megan et al. 2009), and is widely accepted (Fig. 11.1).

11.2.3 Species Richness and Life History Diversity of Nematodes

Nematodes are the most abundant metazoans in the world, often referred to as ‘the most successful animal on earth,’ as four of every five metazoans are considered to be nematodes (Rosenberg 2003; Giblin-Davis et al. 2013). However, their species richness is still very difficult to estimate, because only 25,000 to 30,000 species have been described so far. Thus, the estimation varies among researchers. The most conservative number is 500,000 to 1 million species (Poinar 1983). However, based on recent surveys of plant- and insect-associated nematodes, many species-specific parasites and phoretic associates have been found (Giblin-Davis et al. 2013). Thus, if 5 % to 10 % of insects (and other animals) and higher plants had their species-specific parasites, the species richness of nematodes would be much higher than previous estimations. In addition to these species, there are many free-living soil-inhabiting species and aquatic species, which are estimated to be more divergent than parasites. Therefore, the species diversity of nematodes may exceed 5 million species.

The biological feature of nematodes, such as feeding and habitat preferences, is also very divergent among species. Nematodes can be found in almost every habitat on earth. Free-living nematodes have been recorded from various substrates, such as soil, epiphytes, freshwater, and seawater, and various environments, for example, at a soil depth of 3600 m (Borgonie et al. 2011) and in Antarctica (Freckman and Virginia 1993; Adams et al. 2014). Some plant parasites can inhabit even a desert, feeding on the deep roots of desert plants and bacteria (Freckman and Virginia 1989; Vandegehuchte et al. 2015). Their feeding manners are also divergent, namely, parasitic species of plants and animals, microbe (fungi, yeasts, bacteria) feeders, and predators (Yeates et al. 1993) are well known, and even among parasites, the parasitic manner varies among species. Further, omnivores in the family Diplogastridae show feeding polymorphism, switching their feeding resource from fungi or bacteria to meiofauna, including other nematodes (Ragsdale et al. 2013a; Serobyan et al. 2014; Susoy et al. 2015; Kanzaki 2016).

Ecologically, because of their abundance, free-living nematodes have an important role in soil and marine ecosystems to connect the microbes and larger meiofauna, such as mites, in the nutritional cycle (Yeates et al. 1993). Thus, to evaluate their diversity, functional diversity, that is, species (or molecular operational taxonomic unit, MOTU) inventories, including their ecological function, should be considered.

Nematode distribution is strongly affected by microhabitats. For example, Pinto et al. (2013) suggested, based on their diversity survey of Brazilian mangrove regions, that the nematode fauna was affected by environmental factors of their microhabitats. Also, in the nematode diversity survey in a lowland tropical forest in Costa Rica, nematode fauna associated with epiphytes and soil did not overlap with the associates of soil-inhabiting termites collected at the same sampling sites; that is, termite-associated species inhabited only in (or around) a termite colony, and did not migrate to the soil environment surrounding a termite nest (Powers et al. 2009; Kanzaki et al. 2012a). Further, many genera that are considered as soil-inhabiting plant parasites in the temperate zone were found from epiphytic plants in the survey; the nematode habitat had shifted from soil to epiphytes (Powers et al. 2009).

These results may suggest the difficulty of diversity surveys, that various different environments and microhabitats including potential parasitic or phoretic hosts should be examined and considered while employing several different methodologies to understand the aerial diversity of nematodes.

11.3 Methodologies for Nematode Diversity Survey

11.3.1 Nematodes from Environmental Samples

Basic methodologies for nematode diversity surveys have not been changed for a long time. For example, to evaluate the diversity of soil species, the substrates are collected and nematodes are isolated using a Baermann funnel, sugar floatation, or other methodology (Southey 1986), to identify and count the numbers of recovered nematodes.

Traditionally, the nematodes were identified based on morphological characters, and the identification required the knowledge of nematode morphology, and sometimes, well-preserved adult nematode material, because the species- or genus-level characters are only manifested in adult individuals. Further, specimen examination can become very time-consuming work. After early 2000, the molecular barcoding technique, that is, identification based on species-specific molecular sequences, has been generally used for a diversity survey to avoid some of the pitfalls of morphology-based survey work. There, the nematodes are digested to serve as the polymerase chain reaction (PCR) template DNA (Porazinska et al. 2009). Then the barcoded regions, where partial ribosomal RNA gene sequences are often employed, are amplified, sequenced, and compared with a database to identify the materials to the species level (or genus or family level, in many cases) (Creer et al. 2010). In this type of analysis, knowledge of the morphology and taxonomy, and adult nematode material, are not required. Further, recent pyrosequencing technology and soil DNA extraction methodology allow us to analyze without isolating nematodes from substrate material, so that a nematode assemblage containing many different species can be analyzed at once (Sapkota and Nicolaisen 2015).

In Japan, pyrosequencing (metagenomic) analysis has not been applied for soil or marine nematode diversity so far. Currently, two other barcoding methodologies based on individual sequencing of garden soil (Morise et al. 2012) and forest soil (Akiba and Kanzaki 2014), and a PCR-denaturing gradient gel electrophoresis (DGGE) technique for the diversity survey of agricultural fields (Okada and Ohba 2008; Bao et al. 2012) have been conducted.

Similar methodology can be applied for parasitic nematodes of larger animals using animal dung that contains nematode eggs or dead nematodes, and Tanaka et al. (2014a) successfully applied a metagenomic approach to analyze the helminth fauna associated with wild rats.

However, in both morphological and molecular identifications, biological information of each nematode species or MOTU, such as the host–parasite interaction of each plant-parasitic species, is necessary to evaluate the functional diversity of the community. Nevertheless, at current status, many soil and aquatic nematodes have been registered as simple MOTUs in the sequence database without their biological features, although the animal parasites have been studied for their biological and ecological features because of their practical importance. To expand the applicability of the database to functional diversity studies, extensive taxonomic work including bionomics and molecular phylogenetic analyses is necessary for these soil and aquatic species.

11.3.2 Entomophilic Nematodes

The survey of entomophilic (insect-associated) nematodes is methodologically different from that of soil and plant-parasitic species.

As already mentioned, nematodes are found from almost all ecosystems on Earth. However, although some species have an anhydrobiotic survival stage, for example, *Aphelenchus avenae* (Crowe and Madin 1975), nematodes are basically aquatic or semiaquatic organisms inhabiting the water film on various substrates. Thus, they are vulnerable to dehydration. Further, because of their body size, about 0.5 to 2.0 mm in average length, their mobility is limited. Therefore, nematodes often use other organisms for their shelter or transportation. This feature could be one of the most important evolutionary forces to select for a parasitic life cycle in many different clades. For this purpose, arthropods, especially insects, are the most commonly available hosts because of their ubiquitous distribution and abundancy.

Using nematode phylogeny and biological characters, different types of insect associations have occurred several times independently (Blaxter et al. 1998) (Fig. 11.1), which may also suggest the commonness of nematode–insect associations.

The nematodes associated with insects are generally termed entomophilic nematodes, containing phoretic associates, parasites, parasitoids, and entomopathogens (Poinar 1975; Kanzaki and Kosaka 2009). Phoretic nematodes are associated with insects by using the insect solely for transportation; the nematodes are associated with the insects as their dauer (dormant) stage and do not have any direct nutritional relationship with their carrier insects. These dauer juveniles enter the tracheal system, genital system, digestive system, body cavity, or intersegments of insects. Some phoretic associates are considered to be necromenic species, which propagate on the dead insects feeding on microbes occurring on the host carcass. Parasites enter the body cavity, genital system, or digestive system of insects as the egg, infective juvenile, or infective adult stage, and obtain nutrients from their host insects. The strength of parasitism (virulence, in some cases) varies among species. Some species do not affect the reproduction of their host insect, but others often sterilize or kill their hosts. Parasitoids are somewhat similar to parasites. They infect hosts as eggs or juveniles, develop to late-stage juveniles in the body cavity of the host feeding on the host body, and kill the host. Well-developed late-stage juveniles emerge from dead insects, develop to adults, and mate in wet environments, mostly soil or water. Entomopathogenic nematodes are associated with insect-pathogenic bacteria to kill the host insects. The infective juveniles of the nematodes enter the hosts via mouth, anus, and tracheal system, release the bacteria to kill the insects, and propagate on the bacteria. The life cycles of several parasitic and phoretic nematodes are introduced in Fig. 11.2.

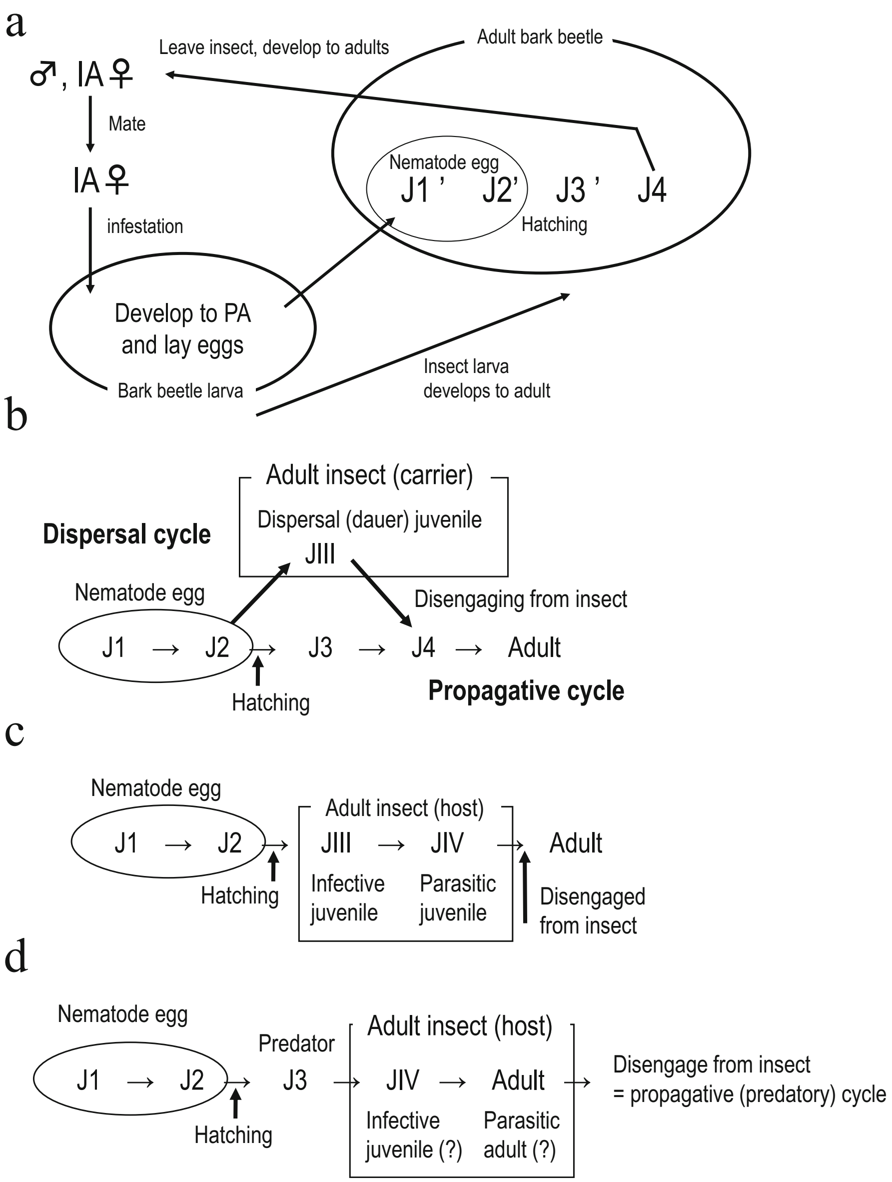


Fig. 11.2 Life cycle of several entomophilic nematodes. (**a**) Parasitic species, *Contortylenchus* spp. (**b**) Phoretic species, majority of *Bursaphelenchus* spp. (**c**) Parasitic species *Parasitaphelenchus* spp. (**d**) Parasite and predator species *Devibursaphelenchus* spp. *J* juvenile stage (*Arabic numerals* indicate propagative; *Roman numerals* dispersal), *IA* infective adult, *PA* parasitic adult. (Modified after Kanzaki and Kosaka 2009)

In contrast to free-living soil nematodes and plant parasites, the number of entomophilic species per sample (= single insect species) is usually low, fewer than ten species, and because of the size of insects, the nematodes can be isolated from individual insects by dissecting them. Therefore, surveys become rather alpha taxonomy-based studies, and it becomes more difficult to construct large species (MOTU) inventories of entomophilic nematodes compared with other groups.

However, during dissection, the insect-associated stage of nematodes, the dauer juvenile, parasitic juvenile, or adult, and organ of the insect harboring the nematodes can be distinguished. Further, the natural habitat of nematodes can be estimated from the biological characters of the insects, such as host habitat and feeding preferences. Therefore, the estimation of biological features of the entomophilic nematodes could be less difficult when compared with other free-living nematodes. The entomophilic nematodes should be examined for more detailed bionomic characters and could prove to be an interesting subject for examining ecological diversity.

11.4 Survey of Entomophilic Nematodes: Several Case Studies

11.4.1 Brief Summary of Previous Work

Poinar (1975) summarized the biological relationships between nematodes and insects with a comprehensive, 150-page host–nematode list. Within these insects, wood-boring insect groups, including bark beetles (Scolytidae), weevils (Curculionidae), longhorn beetles (Cerambycidae), and scarabaeid beetles (Scarabaeidae), have been examined for a long time in European countries and the United States to explore for biological control agents because these insects are important as forest and agricultural pests (Rühm 1956; Massey 1974).

Although systematic surveys of entomophilic nematodes have not been conducted in the Asian region except for several ongoing studies, several case studies are introduced here.

11.4.2 Bark and Ambrosia Beetles, Weevils, and Longhorn Beetles

The nematode fauna associated with wood-boring insects, especially bark beetles, has been examined throughout the world and currently represent the best studied group among all insects. In Japan, several phoretic species have been taxonomically described, and many other unidentified parasites and phoretic associates have been recorded.

Shimizu et al. (2013) examined the nematode association of the coleopteran insects emerging from dead Japanese red pine (*Pinus densiflora*) logs, and reported seasonal changes of nematode association ratio of a bark beetle species, *Dryocoetes uniseriatus*. The beetle was associated with six nematode species including two phoretic fungal feeders, *Bursaphelenchus rainulfi* and *B. sinensis*, an insect parasite–predator species, *Devibursaphelenchus eproctatus*, an insect parasite–bacterial feeder, *Parasitorhabditis* sp., a phoretic bacterial feeder, *Micoletzkya japonica*, and a parasite, *Contortylenchus* sp. The nematodes were found from a sheath-like tissue formed on the back side of the elytra (nematangia) (dauer juveniles of two *Bursaphelenchus* spp. and adult and late-stage juvenile of *D. eproctatus*) (Fig. 11.3), the underside of the elytra, and beneath the scutellum (*M. japonica*), hindgut (*Parasitorhabditis* sp.), and body cavity (*Contorylenchus* sp.). Their seasonal pattern also differed among species, and two parasitic species (*D. eproctatus* and *Contortylenchus* sp.) (Fig. 11.3) dominated during the early season, whereas *Parasitorhabditis* and *M. japonica* dominated in the late season, probably because the phoretic mites occupied the backside of the elytra in the late season.

In addition, several researchers conducted alpha-taxonomic studies on these nematodes, and described several phoretic species from those beetles, namely,

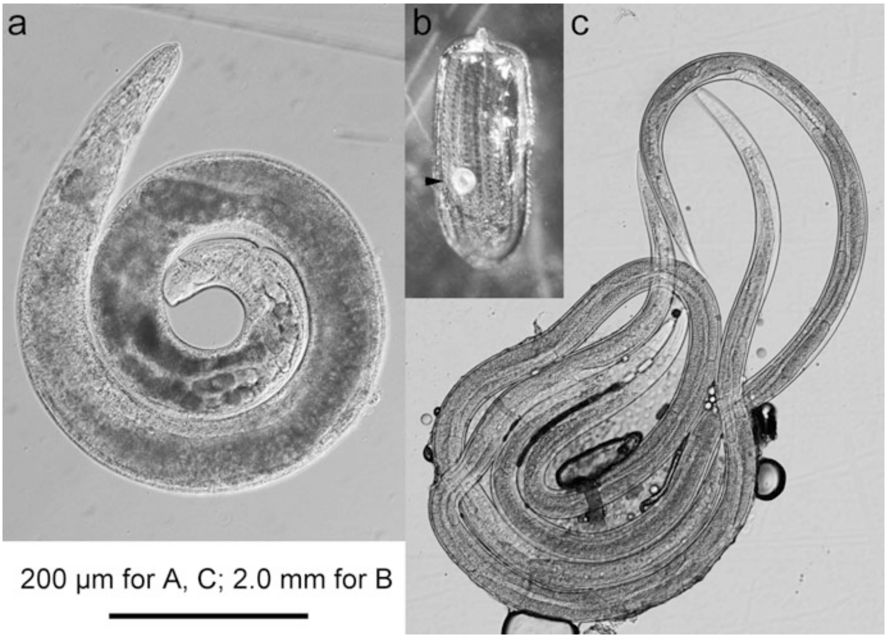


Fig. 11.3 Two parasitic species isolated from *Dryocoetes uniseriatus*. (**a**) *Contortylenchus* sp. female. (**b**) Elytra of *D. uniseriatus* harboring nematangea (*arrowhead*). (**c**) *Devibursaphelenchus eproctatus* emerging from nematangea. (Modified after Kanzaki and Kosaka 2009 and Shimizu et al. 2013)

phoretic fungal feeders, *Bursaphelenchus* spp., including an invasive forest pest, *B. xylophilus* (Fig. 11.4), from the tracheal system of longhorn beetles and weevils, and underside of elytra of bark and ambrosia beetles (Mamiya and Kiyohara 1972;

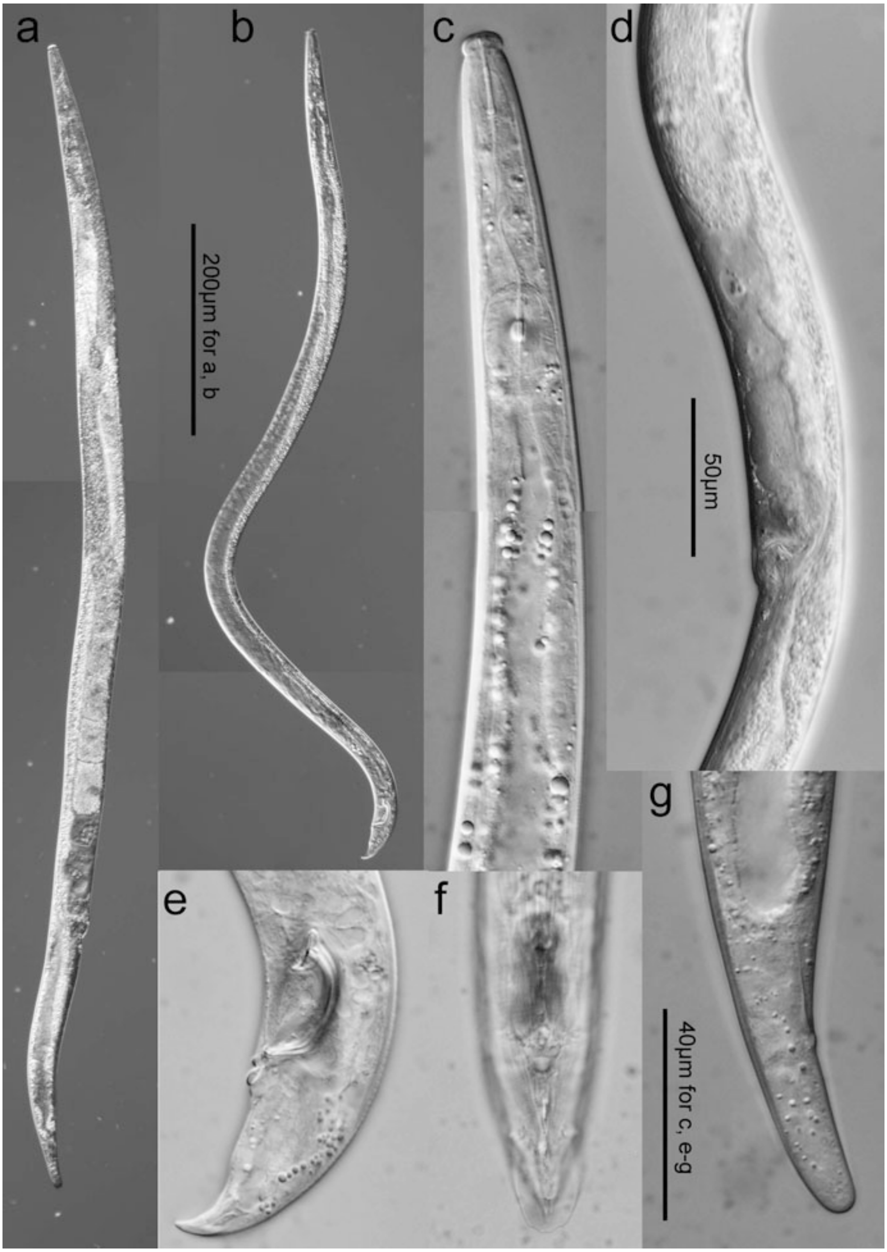


Fig. 11.4 *Bursaphelenchus xylophilus* associated with *Monochamus* spp. (**a**) Female. (**b**) male. (**c**) Anterior part of adult. (**d**) Vulval region of adult female. (**e**) Male tail showing spicule. (**f**) Ventral view of male tail showing bursal flap. (**g**) Lateral view of female tail

Mamiya and Enda 1979; Kanzaki and Futai 2003, 2005; Kanzaki et al. 2000, 2007a, 2008a, b, 2010a, 2011a, 2012b; Tanaka et al. 2014b); a phoretic bacterial feeder, *Rhabditolaimus* spp., from the genital capsule and ovipositor of longhorn beetles (Kanzaki and Futai 2004), and the elytra of bark and ambrosia beetles (Kanzaki et al. 2006); a phoretic bacterial feeder, *Diplogasteroides* spp., from the genital capsule and ovipositor of longhorn beetles (Kanzaki et al. 2002, 2013a, 2015a, 2016c; Kanzaki and Ide 2016); omnivores, *Neodiplogaster* spp., from the tracheal system of a longhorn beetle and the elytra of an ambrosia beetle (Kanzaki et al. 2008c); and internal parasites, *Contortylenchus* spp., unidentified allantnematid parasite, and *Ektaphelenchoides spondylis*, from the body cavity of longhorn and bark beetles (Kosaka and Ogura 1993; Kanzaki et al. 2009a, 2016a).

Within these phoretic and parasitic nematodes, the genus *Bursaphelenchus*, mostly phoretically associated with coleopteran insects, is well documented for their insect association. Their carrier preference seems related with their phylogeny, that is, the *Bursaphelenhcus* clade, although it contains taxonomically different genera, is separated roughly into three groups: a first clade that is associated with bark beetles and weevils, a second clade that is associated with various insects including soil-dwelling bees, and a third clade that is mostly associated with longhorn beetles (Fig. 11.5).

More detailed phylogenetic comparisons between phoretic nematodes and their carrier bark beetles were conducted by Susoy and Herrmann (2014). They compared the phylogenetic trees of *Micoletzkya* spp. and their carrier bark beetles, demonstrating that the nematodes have clear carrier specificity and that their speciation is highly influenced by that of bark beetles; there was a clear co-phylogenetic relationship.

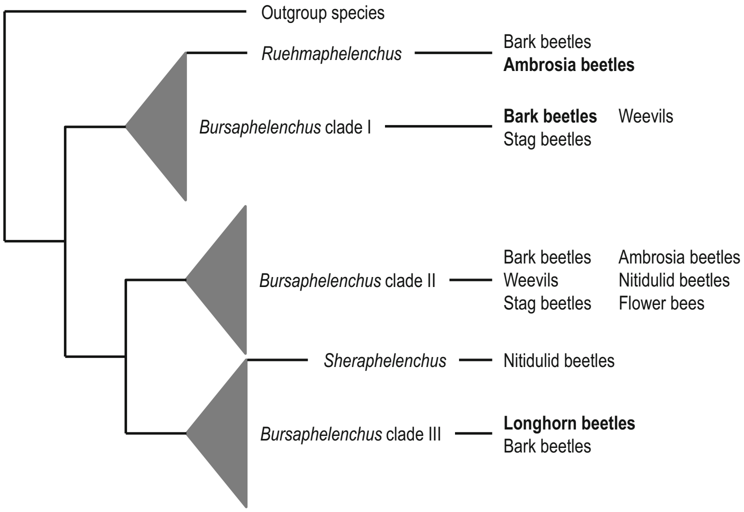


Fig. 11.5 Relationship between major clades in *Bursaphelenchus* and its related genera, with their carrier preference

The other interesting genus (clade) is *Ruehmaphelenchus*. The genus had been relatively rare, with only two species known until recently (Braasch et al. 2006). However, our recent survey revealed that the genus is mostly associated with ambrosia beetles (Kanzaki et al. 2013b, 2015b), probably because of undersampling of ambrosia beetles; that is, most of the bark and ambrosia beetle surveys were conducted in the temperate zone (European countries and United States), but the ambrosia beetles are more abundant in warm-temperate to tropic areas (Nobuchi 1977). Thus, ambrosia beetle surveys in warmer regions may yield more taxa from this lineage.

The nematodes found in Japanese wood-boring insects are common to those found in Europe and the United States at the genus level (Rühm 1956; Massey 1974). Thus, the results suggested by Susoy and Herrmann (2014) may be applicable to many other wood-boring beetle associates; more different species belonging to the same genera will be found from Japanese native beetles.

The other important feature of wood-boring associated nematode fauna is that the fauna contains many fungal feeders, such as *Bursaphelenchus* spp., and parasites derived from fungal feeders, for example, *Devibursaphelenchus* and *Ektaphelenchus*. These beetles prefer relatively newly dead trees, where the xylem tissues have not decomposed, and the substrates provide a carbon-rich environment suitable for fungi.

11.4.3 Stag Beetles

Currently, only some preliminary results have been published for Japanese stag beetle-associated nematodes (Kanzaki et al. 2011b, 2012c, d, 2014a, 2015c, 2016b).

Kanzaki et al. (2011b) examined the nematode fauna, dissecting more than 100 individuals of stag beetles including eight species, *Prismognathus angularis*, *Prosopocoilus inclinatus*, *Lucanus maculifemoratus*, and five *Dorcus* spp., collected from the Honshu and Kyusyu Islands of Japan. Eleven species (morpho- or genotypes) of nematodes were found that mostly consisted of bacteria feeders and omnivores; except for one fungal feeder, *Bursaphelenchus tadamiensis*, all other nematodes belonged to the family Diplogastridae including four omnivores (*Allodiplogaster* cf. *lucani*, *Pristionchus exspectatus*, *Parapristionchus giblindavisi*, and *Koerneria* cf. *luziae*), three bacteria feeders (two *Pseudodiplogasteroides* spp. and *Rhabditidoides* sp.), and three unidentified diplogastrids (Fig. 11.6). In addition to these species, some additional specimens from Okinawa (*Dorcus titanus sakishimanus*), were also associated with a phoretic fungal feeder, *Bursaphelenchus sakishimanus*, and omnivores and bacterial feeders belonging to the families Diplogastridae and Rhabditidae (Kanzaki et al. 2015c; Kanzaki, unpublished observations); thus, the species composition was similar among the northern Honshu Islands through Okinawa.

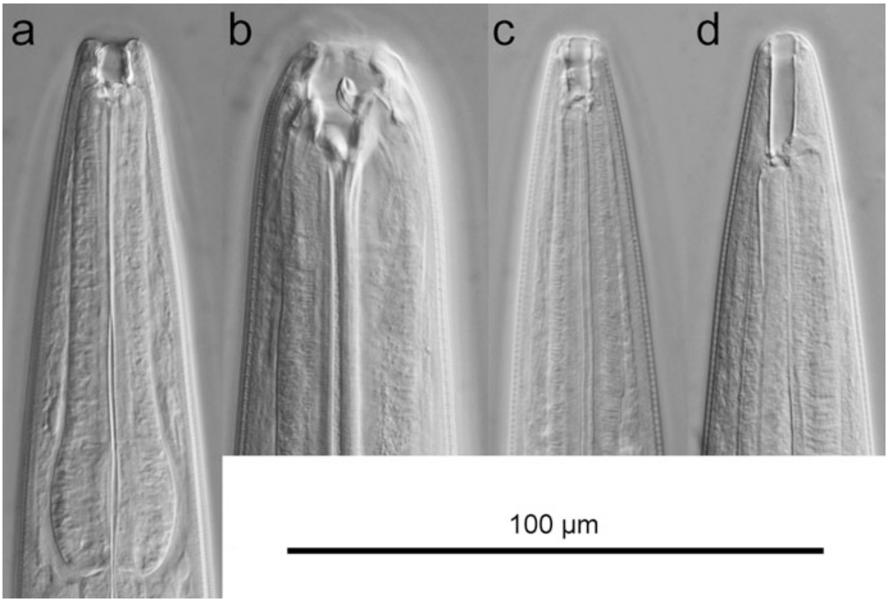


Fig. 11.6 Stomatal regions of stag beetle-associated nematodes. (**a**) *Pristionchus exspectatus*. (**b**) *Allodiplogaster* cf. *lucani*. (**c**) *Pseudodiplogasteroides* cf. *composites*. (**d**) *Rhabditidoides* sp. (Modified after Kanzaki et al. 2011b)

The species composition of Japanese stag beetle associates was also similar to that of stag beetles in Europe. Körner (1954) reported several diplogastrid nematodes (*Allodiplogaster*, *Koerneria*, and *Pseudodiplogasteroides*) from the European stag beetles *Lucanus cervus*, *Dorcus parallelopipedus*, *Sinodendron cylindricum*, and *Systenocerus cribatus*. Within these nematodes, three species, *A. lucani*, *K. luziae*, and *P. compositicola*, were morphologically identical to the Japanese species, and are considered to be cryptic species, or relatively cosmopolitan. Thus, as with curculionid and cerambycid associates, the nematode fauna seems to be shared at the generic level.

However, when compared with the curculionid and cerambycid associates, the composition of the stag beetle-associated nematode species is more inclined toward bacterial feeders and omnivores. Stag beetles (and some other Scarabaeoidea) utilize wet decaying woods (and rich soil), which are more suitable for bacterial growth. Thus, the nematode fauna is probably affected by the feeding and oviposition preferences of their carrier insects.

11.4.4 Hymenoptera

The order Hymenoptera, including bees, wasps, and ants, is very divergent including eusocial to solitary species, and specialized fig pollinator mutualists, fig wasps. Although no systematic survey has been conducted in Japan (and other areas, because the order is too divergent to consider), some species have been examined for nematodes by several researchers.

As a general tendency, eusocial bees and wasps have only few internal nematode parasites (Poinar 1975; Kaiser 1987; Kanzaki et al. 2007b), and solitary species are often associated with phoretic fungal feeders and omnivores (Poinar 1975; Giblin and Kaya 1983, 1984; Giblin et al. 1984; Giblin-Davis et al. 1993, 2005, 2010; Hazir et al. 2007, 2010, 2015; Kanzaki 2006; Kanzaki et al. 2009b, 2010b, 2015d), possibly because of the nesting behavior of the bees and wasps. Many eusocial species have dry aerial nests, where microbe feeders cannot propagate, and solitary species often nest in soil or dead trees, regular habitats of microbe-feeding nematodes.

In Japan, only a few nematode species have been reported from hymenopteran hosts, fitting the general pattern seen elsewhere, that is., internal parasites, *Sphaerularia* spp. from hornets (*Vespa* spp.) and bumblebees (*Bombus* spp.) from many different areas in Japan (Kanzaki et al. 2007b; Kosaka et al. 2012) (Fig. 11.7), a fungal feeding phoretic associate, *Aphelenchoides xylocopae* from the large carpenter bee, *Xylocopa appendiculata circumvolans* from Kyoto and several other places (Kanzaki 2006), and an unidentified *Allodiplogaster* species from a soil-dwelling bee, *Andrena longitibialis* from Hakodate, Hokkaido (Kanzaki et al. 2015d).

In contrast, many mermithid parasitoids and rhabditid bacterial feeders have been reported from ants (summarized by Poinar 1975), probably because of their underground nests, often in association with leaf litter, but only a little information has been published concerning ant-associated nematodes in Japan (Kubo et al. 2016).

Fig wasps are significantly specialized pollinators associated with *Ficus* syconia. The nematode fauna associated with these wasps (and host figs) is also considerably specialized. Two genera, *Parasitodiplogaster* and *Schistonchus*, have been known for a long time from the American, African, and Eurasian continents and Australia (Gasparrini 1864; Martin et al. 1973; Poinar 1979; Poinar and Herre 1991; Bartholomaeus et al. 2009; Wöhr et al. 2015). *Parasitodiplogaster* appears to be an insect parasite, wherein parasitic juveniles enter the body cavity of fig wasp females and develop there after the host finishes pollination and oviposition activities (Giblin-Davis et al. 1995), and *Schistonchus*, a polyphyletic genus derived from ancestral fungal feeders, which is phoretically associated with the wasps and feeds on the plant tissue inside fig syconia (Giblin-Davis et al. 1995; Vovlas and Larizza 1996; Center et al. 1999; Davies et al. 2015). In addition to these two or more genera, recent surveys added three genera, *Ficotylus*, *Teratodiplogaster*, and *Bursaphelenchus*, and some other genera as fig and potential fig–wasp associates (Anand 2005; Davies et al. 2008; Kanzaki et al. 2009c, 2014b; Giblin-Davis

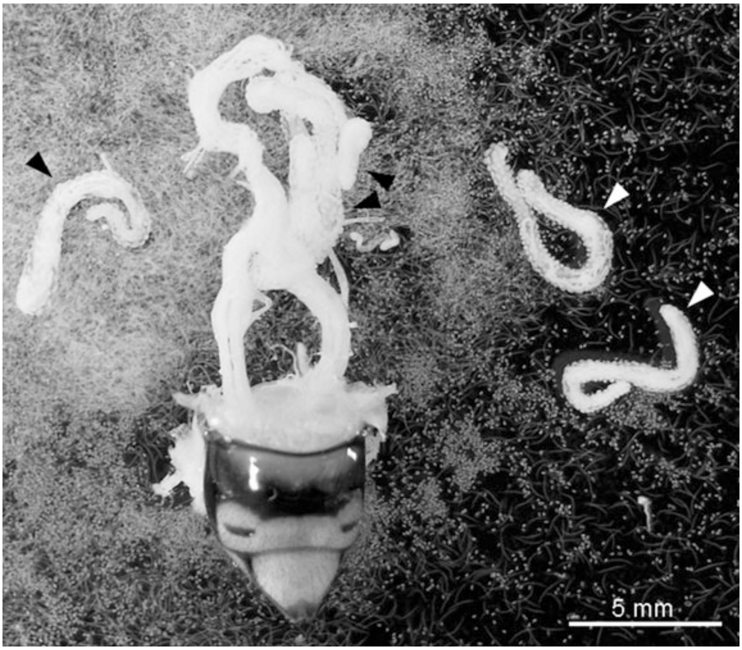


Fig. 11.7 *Sphaerularia vespae*, a parasite of hornets. Females everts their uterus to be 'uterium' (*arrowhead*), a parasitic form specialized for oviposition. Small parasitic juveniles and eggs are also found from the body cavity of host hornets. (Modified after Kanzaki et al. 2007b)

et al. 2014), and several more genera, unidentified predatory nematodes and undescribed rhabditid species, have been found from the figs.

In Japan, at least five genera have been confirmed, namely *Teratodiplogster* (*T. variegatae* from *F. variegata* in Ishigaki, Okinawa) (Fig. 11.8), *Schistonchus* (undescribed species from *F. variegata* and several other *Ficus* spp.), *Bursaphelenchus* (*B. sycophilus* from *F. variegata* in Ishigaki, Okinawa), predatory diplogastrid close to *Pristionchus* (from *F. variegata* in Ishigaki, Okinawa), and bacteria-feeding species close to *Caenorhabditis* (from *F. septica* in several islands in Okinawa) (Kanzaki et al. 2014b, c, d). As far as we know, *Schistonchus* is a cosmopolitan genus, although it is obviously polyphyletic (Davies et al. 2015), and it is not surprising that the genus occurs in Japan. However, *Bursaphelenchus* spp. are, as already mentioned, mostly associated with coleopteran wood borers, and a few species are associated with soil-dwelling bees. Thus, the ecological and physiological mechanisms of host switching in *B. sycophilus*, which is not phylogenetically close to any of the bee-associated *Bursaphelenchus* spp., are unknown. In addition, similar *Bursaphelenchus* species have been found from some African figs (Kanzaki et al., unpublished observation). *Teratodiplogaster* has been reported from Africa (Martin et al. 1973; Kanzaki et al. 2012e), Australia (Kanzaki et al. 2009c), Indonesia (Sriwati et al. 2013), Vietnam (Kanzaki et al. 2012f), and Japan (Kanzaki et al. 2014d), but have not been recovered from the American

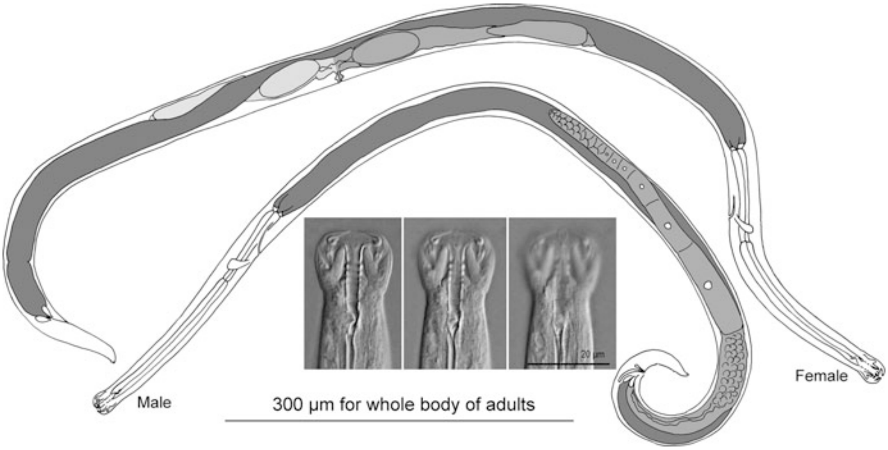


Fig. 11.8 *Teratodiplogaster variegatae*, an associate of fig wasp and fig. Male, female, and adult stomatal region. (Modified after Kanzaki et al. 2014d)

tropics and subtropics regardless of many field survey attempts. Considering the isolation pattern at the genus level, fig-wasp-associated nematodes in Japan are part of a large phylogeographic group extending through Africa to the West Pacific region in association with certain *Ficus* lineages.

11.4.5 Dung- and Carcass-Associated Beetles

Animal dung and carcass are the most nitrogen-rich substrates in many ecosystems, and many insects and larger animals utilize these resources. In coleopteran insects, dung beetles (Scarabaeoidea), carrion beetles (Silphidae), rove beetles (Staphylinidae), and several other families are typically associated with these substrates.

Currently, the field survey of nematode associates of these beetles has just been started by the author and colleagues, and only preliminary information has been published, except for a species description and some abstracts. In other countries, the nematodes associated with these insects are characterized as phoretic bacterial feeders and omnivores and parasitic species derived from fungal feeders and bacterial feeders, for example, *Pristionchus*, *Koerneria*, *Fictor* (omnivore), *Rhabditoides*, *Pelodera* (bacteria feeder), *Peraphelenchus* (Fig. 11.9), *Entaphelenchus* (internal parasites derived from fungal feeders), and spirurid parasites (Wachek 1955; Weller et al. 2010). This species (generic) composition is probably representative of the environmental character and available niches in dung, wet and rich in nutrients appropriate for the propagation of bacteria.

As for the other insect groups, the nematode fauna associated with these beetles in different locations in Japan is similar to European associates at the generic level;

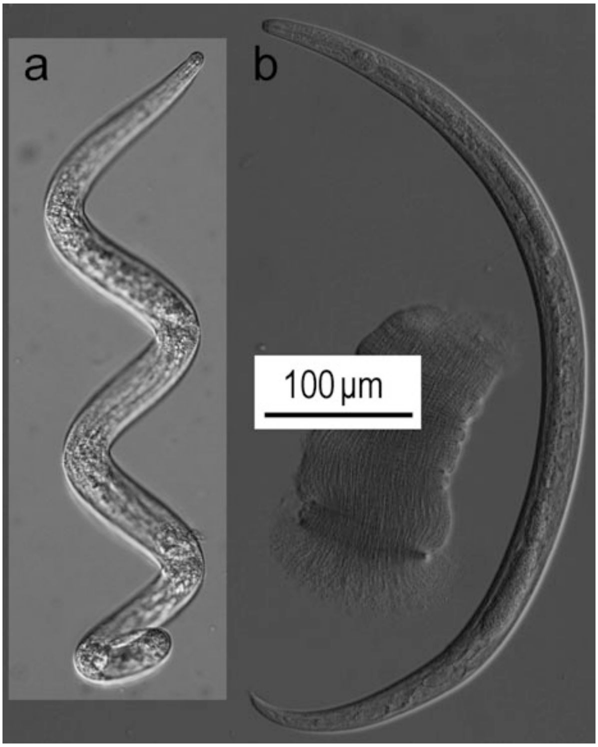


Fig. 11.9 *Peraphelenchus orientalis*, an internal parasite of carrion beetles, *Nicrophorus* spp. (**a**) Male. (**b**) Infective (*young*) female. (Modified after Kanzaki et al. 2013c)

for example, *Pristionchus*, *Fictor*, *Rhabditoides*, *Peraphelenchus*, and an unidentified parasitic species have been isolated from these insects collected in Japan (Kanzaki et al. 2013c; Kanzaki, personal observation).

11.4.6 Termites and Cockroaches

Presently, termite–nematode associations have not been studied in detail; several taxonomic studies have been conducted in European countries and the United States (Leidy 1877; Snyder in Banks and Snyder 1920; Massey 1971; Fürst von Lieven 2003; Sudhaus and Koch 2004; Fürst von Lieven and Sudhaus 2008; Kanzaki et al. 2009d, e, 2010c), and a few focal sampling studies have been conducted on Corsica Island (Fürst von Lieven and Sudhaus 2008), Hawaii (Pemberton 1928), and in the American tropics and subtropics (Kanzaki et al. 2012a). On Corsica Island, Fürst von Lieven and Sudhaus (2008) examined many colonies (number not provided) of *Reticulitermes lucifagus* for more than 5 years, and recognized 18 genera (more than 20 species) of nematodes including coincidental and casual associations. There, most of the nematodes were considered to be phoretic bacterial feeders and omnivores, with only a few fungal feeders and parasitoids being reported. In contrast, Kanzaki et al. (2012a) examined approximately 50 species (~300 colonies) of termites, and recognized 15 phylogenetic groups (= tentatively considered as genera) (~50 MOTUs). In both studies, the nematodes were mostly phoretic bacterial feeders and omnivores, with a few phoretic fungal feeders and parasites being reported. The nematode fauna seems well adapted to the nesting habitats of subterranean termites. Dry and damp wood termites do not have many nematode species, being associated with several phoretic bacterial feeders, mainly *Poikilolaimus* spp. and *Halicephalobus* spp., versus subterranean and arboreal termites, which were associated with many groups of nematodes.

In Asian countries, several field surveys were conducted, and brief species lists (morphotypes and/or genotypes) have been provided, wherein eight phoretic genera including two omnivores (*Oigolaimella* and *Pristionchus*), four bacterial feeders (*Poikilolaimus*, *Halicephalobus*, *Bunonema*, and *Mesorhabditis*), and two fungal feeders (*Pseudaphelenchus* and *Aphelenchoides*) were reported (Kanzaki et al. 2009f). Thereafter, three species have been taxonomically described, namely, *Poikilolaimus (Po.) carsiops* from *Neotermes koshunensis* from Taiwan (Kanzaki et al. 2011c) (Fig. 11.10), *Pseudaphelenchus (Ps.) sui* from *Coptotermes formosanus* from Okinawa and *Ps. scheffrahni* from *Nasutitermes takasagoensis* from Taiwan (Kanzaki et al. 2014e).

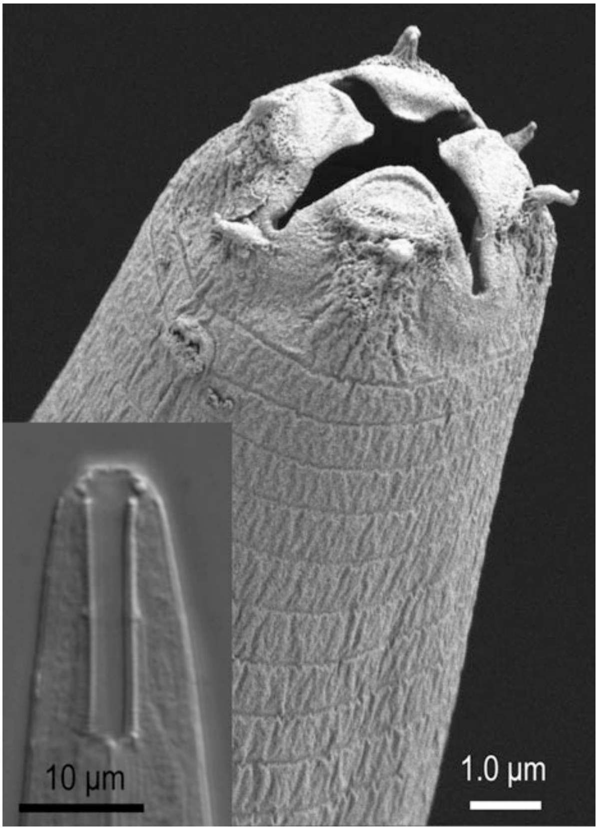
Comparing the nematodes at the generic level, the fauna in three different regions, the American tropics and subtropics, Corsica Island (Europe), and Okinawa and Taiwan (East Asian subtropics), are very similar to each other: five dominant omnivores and bacterial feeders (*Oigolaimella*, *Poikilolaimus*, *Halicephalobus*, *Bunonema*, *Mesorhabditis*) are common in all three areas, and further, two other genera *Pseudaphelenchus* (Asian and American tropics and subtropics) and *Pristionchus* (Corsica Island and Asian subtropics) are common in two of the three regions.

Based on the feeding habitats of termite-associated nematodes, the nematode fauna is similar to that associated with soil-inhabiting insects (summarized in Poinar 1975), which makes sense relative to the life history and habitat preference of the carrier insects.

Cockroaches are also generally known to be associated with nematodes (Poinar 1975). Most cockroach associates are pinworms (Thelastomatidae) parasitizing the hindgut of cockroaches, and an external parasite, *Acugutturus parasiticus*, which is derived from fungal-feeding nematodes, has been found from Central America (Hunt 1980). Interestingly, no phoretic associate has been described from cockroaches, although this could be the result of undersampling.

In Japan, only a few projects have examined cockroach-associated nematodes so far. Ogata et al. (1975) confirmed a pinworm species, *Leidynema appendiculata* (Fig. 11.11) from *Periplaneta* species, and Ozawa et al. (2014) reported the generality of *L. appendiculata* parasitism of an invasive cockroach species, *P. fuliginosa*. In addition to those publications, the author confirmed that several cockroach species are parasitized by pinworms, namely, *Periplaneta* spp., *Opisthoplatia orientalis*, *Panesthia angustipennis spadica*, *Rhabdoblatta*

Fig. 11.10 Stomatal region of *Poikilolaimus carsiops*, a phoretic associate of a dampwood termite (Kalotermitidae) shown by micrographs and scanning electron micrographs. (Modified after Kanzaki et al. 2011c)



yayeyamana, and *Pycnoscelus surinamensis*, although the nematodes have not been identified (Kanzaki, unpublished observation). Contrastingly, no nematode has been recovered from several *Blattera* species in Japan, but this could be the result of undersampling, because pinworm infections of *Blattera* species have been reported from many different places in the world.

11.4.7 Entomopathogenic Nematodes

Research on insect pathogens (entomopathogenic nematodes, EPN) is different in scope from that done on other entomophilic nematodes, namely because EPNs have practical uses as biological control agents in agricultural, horticultural, urban, and other applicatons. Thus, to explore and prospect for potential biological control agents, field surveys of EPN have been conducted all over the world. Generally, the EPN consists of two different lineages represented by two genera, *Steinernema* and *Hererorhabditis*. Regardless of their phylogenetic differences, the life history traits

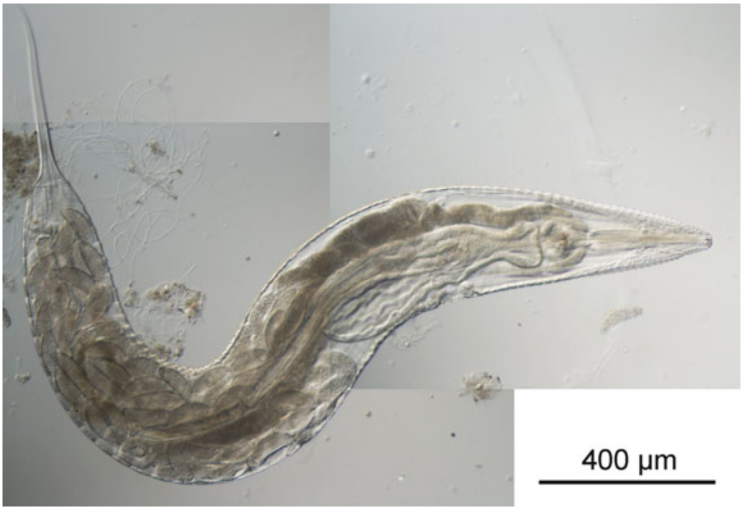


Fig. 11.11 Adult female of *Leidynema appendiculata*, a gut parasite of the cockroach, *Periplaneta* spp. (Photographed by Sota Ozawa, Chubu University)

are clearly convergent, and those genera utilize the insect pathogenic bacterial genera, *Xenorhabdus* and *Photorhabdus*, respectively.

Field surveys of EPN have also been conducted in Japan, and three species, *Steinernema kushidai*, *S. litorale*, and *S. ashiuense*, have been taxonomically described (Mamiya 1988; Yoshida 2004; Phan et al. 2006). Systematic field surveys and molecular characterizations of the EPNs were conducted by Yoshida et al. (1998) and Kuwata et al. (2006). Yoshida et al. (1998) examined more than 1400 soil samples from 266 localities using a bait trap (*Galleria*), and obtained 142 isolates of EPNs including the two representative genera. Then, these isolates were molecularly characterized with PCR-RFLP profiles, and separated into eight *Steinernema* spp. and two *Heterorhabditis* spp., demonstrating that *Heterorhabditis* spp. prefers warmer regions compared with *Steinernema*. Kuwata et al. (2006) examined the co-phylogenetic relationship between *Steinernema* spp. and their associated *Xenorhabdus* spp. using ten species of *Steinernema* spp. isolated from Japan. Comparisons using internal transcribed spacer (ITS) sequences of the nematodes and 16S ribosomal RNA of the bacteria showed that the phylogenetic relationships were similar to each other, that is, co-phylogenetic relationship were apparent, with some exceptions, probably because of host switching.

Currently, some of these Japanese species have not been taxonomically described; however, based on molecular sequences, several undescribed species seem to be distributed in Japan.

11.4.8 Other Nematodes Associated with Insects and Arthropods

Several other entomophilic nematodes have been described from Japan, and some of them have been studied in detail as the subject of physiological and ecological research.

A bacteria feeder, *Caenorhabditis japonica*, is phoretically associated with the burrowing bug, *Parastrachia japonensis*, and it has many characteristic biological features, including host-specific phoretic association and long-term survival of dauer larvae, which are probably regulated by chemical compounds released from its carrier bug, and negative gravitactic behavior (Tanaka et al. 2012; Okumura et al. 2013a, b). Because *C. japonica* belongs to the genus *Caenorhabditis*, some of the genetic information obtained from the model organism, *C. elegans*, could be applicable, and the species is expected to be an interesting research model to examine the aforementioned physiological and behavioral traits.

Hemiptera including the burrowing bug are not common as hosts (carriers) of nematodes, and only a few parasitoids (e.g., *Agamermis unka* parasitizes a plant hopper) have been described, and almost no nematodes have been reported from shield bugs (Poinar 1975). Thus, the species-specific phoretic association of *C. japonica* is hypothesized to have occurred as an apomorphic biological character in this nematode species.

Aihara (2001) and Tsuda and Futai (1999, 2005) examined the nematode association of fungal gnats (Diptera: Mycetophilidae), and described four *Iotonchium* species: *I. cateniforme*, *I. laccariae*, *I. russulae*, and *I. unglatum*. The nematode has two phases, an entomoparasitic phase that parasitizes their host fungal gnats and a mycophagous phase that feeds on their host mushroom. *Iotonchium unglatum* is an interesting species because it forms nematode galls on the mushroom of nematode-trapping fungi, *Pleurotus* spp., and feeds on the fungal tissue (Tsuda et al. 1996). The genus has been reported from United States and European countries as the entomoparasitic/mycophagous species, associated with fungal gnats and their host mushrooms (Poinar 1975).

Only a few reports have been published about nematode association with other arthropods in Japan. Hunt (1998) described a *Rhigonema* species, *R. pilosum*, from millipedes collected from Ryukyu Islands. When the current author examined several millipede species from Kyusyu and Okinawa, the same *Rhigonema* species, pinworms, and several phoretic bacteria feeders and omnivores were isolated (Kanzaki et al., unpublished observations). Thus, millipede-associated nematodes are expected to be found common in Japan when a systematic survey is conducted.

11.4.9 Determination Factors of Nematode Fauna

There are probably two important factors to determining the nematode fauna associated with a particular group of insects: first, phylogenetic relationships, namely, the co-speciation of host (carrier) and parasite (phoretic associate), and second, co-adaptation associated with habitat preference of the host (carrier) insect.

Phylogenetically, there are several co-speciation/co-evolution studies on host (carrier)–parasite (phoretic associate) relationships concerning nematodes. Kanzaki and Futai (2002) examined the intraspecific phylogenetic relationship of a phoretic fungal feeder, *Bursaphelenchus conicaudatus*, and its carrier longhorn beetle, *Psacothea hilaris*, and demonstrated their co-speciation was affected by several geographic events in the Ryukyu Archipelago. Susoy and Herrmann (2014) examined the phylogenetic relationship of the phoretic omnivores, *Micoletzkya* spp. and their carrier bark beetle species, and proved the co-speciation relationship in this phoretic system (see earlier). These two studies suggest that, at least at the generic or lower taxon level, the phylogenetic relationship can become an important factor affecting the nematode fauna, whereas, as already mentioned, the nematode fauna seems strongly correlated with habitat preference of their host (carrier) insects. Phoretic relationships occur relatively easily, because there is no direct nutritional relationship between nematode and insect; that is, it may occur accidentally as the dauer stage (dormant) nematode sticks to the surface of insects, and physiological adaptation, which would be required for parasites, is not necessary for this type of accidental transmission from a site of diminished resources to the new host breeding site where more resources are available.

Therefore, it is assumed that the phoretic relationships occurred accidentally between nematodes and insects when sharing the same habitat, and then, nematodes adapted gradually by synchronizing their life histories to insects. This event may have occurred many times independently to form the assemblages of nematodes in each insect group, and then co-speciation or association by descent occurred in each species.

11.4.10 Geographic Distribution Pattern of Entomophilic Nematodes

As already discussed, the nematode fauna associated with each group of insects is common among different regions at the generic level. However, there is only a little information about the geographic distribution of entomophilic nematodes at species level, probably because of difficulties in exchanging the materials among countries. Presently, phoretic omnivores, *Pristionchus* spp., have been examined for their species-level phylogeographic relationships.

The genus *Pristionchus*, including the biological model *P. pacificus*, is one of the most interesting satellite model systems, that is, a comparative system of the model organism, *Caenorhabditis elegans*, and its close relatives (Sommer 2009), and many species have been collected from many different countries and kept as laboratory cultures at the Max Planck Institute (http://sommerlab.org/home.html).

Because the members of this genus are morphologically very similar to each other with significant intraspecific morphological variability, there appear to be many cryptic species complexes. Thus, the species delimitation requires use of the biological species concept, that is, mating study, molecular phylogenetic analyses, and other biological, developmental, and physiological information (Herrmann et al. 2006; Kanzaki et al. 2012g, 2013d, e; Ragsdale et al. 2013a, b). During these biological comparisons, it was found that the distribution range of gonochoristic (male/female) species is rather regional, whereas hermaphroditic (male/hermaphrodite) species distribute more widely. For example, the satellite model *P. pacificus* is a hermaphroditic species that has been isolated from several different continents, and its close relatives, *P. exspectatus*, *P. arcanus*, and *P. japonicus*, have been isolated only from Japan, regardless of dense taxon samplings (summarized in Ragsdale et al. 2015). Further, the other clades in the genus containing gonochorists and hermaphrodites showed a similar pattern (Ragsdale et al. 2015). In addition to the distribution range, the range of natural carrier insects (and other invertebrates) seems wider in hermaphroditic species compared with gonochorists (Ragsdale et al. 2015) (Fig. 11.12).

Dense and systematic taxon sampling such as that done for *Pristionchus* has not been conducted for any other entomophilic nematodes so far. However, if this phenomenon is universally applicable to other entomophilic nematode genera, then most of the gonochoristic entomophilic nematodes recovered from Japan could be undescribed species.

11.5 Perspectives on Entomophilic Nematode Diversity in Japan

Despite its species richness, the species diversity of nematodes has not been understood so far. Even in the entomophilic nematodes, a small biological category of the phylum, almost all newly isolated species are undescribed. Presently, isolation of more nematode species from more different habitats and microhabitats (substrates) followed by molecular characterization with elucidation of biological characters (ecological function) would be a practical way to understand nematode diversity. However, in fact, it is time consuming and difficult to bring this kind of work to fruition. The current situation is quite daunting for the very few trained nematode taxonomists. Some possible future studies on entomophilic nematodes in Japan Islands follow.

One of the most characteristic features of the Japan Islands is the diversity of environments: the chain of islands is quite long from north to south compared with its land area, including cool temperate through subtropical islands, and therefore the

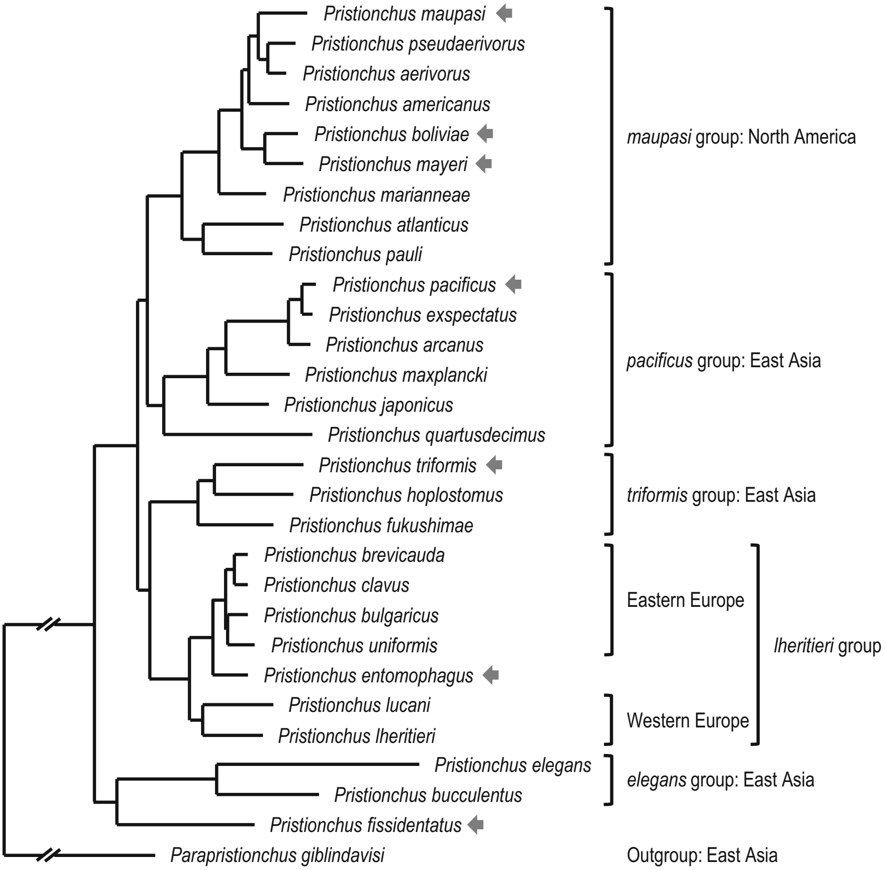


Fig. 11.12 Phylogeographic pattern of *Pristionchus* spp. The genus is separated into several clades, which are in accordance with the type locality of each species, except for the hermaphroditic species (indicated by *arrows*) that are mostly distributed widely

species richness of insects is high relative to the land area because of gene flow fragmentation. This concept would suggest that the diversity of entomophilic nematodes is also potentially high. As noted, the generic composition of entomophilic nematodes is likely similar to those to other areas, and the information obtained from European countries and United States, from mostly cool to moderate temperate zones, could directly be applied to the Japanese entomophilic nematode fauna. Thus, the nematode identification should be relatively easy at the genus level, which should enable estimates of the biological characters for ecological studies.

On the other hand, because the nematode taxonomy and diversity studies were mostly conducted in European countries, including Russia, and United States, the information about tropical and subtropical nematodes has not been sufficient when compared with the temperate zones. Therefore, the presence of subtropical regions in the country could be an advantage for material collections for nematodes (and almost all other biological studies). Surveys in warm temperate (Southern Kyusyu) to subtropical islands (Okinawa) may yield more characteristic new lineages that could be scientifically (and practically) interesting. In fact, several interesting species have been found from the warm regions of Japan Islands, such as *Pristionchus exspectatus*, an interesting comparative species of *P. pacificus* (Ragsdale et al. 2013; Rödelsperger et al. 2014), and *Bursaphelenchus okinawaensis*, a potential satellite model system of fungal-feeding nematodes with a different reproductive strategy (hermaphroditism) (Shinya et al. 2014).

Although their study is in its infancy, nematodes are very interesting and potentially lucrative biological resources for applied science. To utilize these resources effectively, wide-ranging systematic surveys should be first conducted, followed with wider research networking to best apply the myriad discoveries and potential innovations resulting from these important resources.

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References

Adams BJ, Wall DH, Virginia RA, Broos E, Knox MA (2014) Ecological biogeography of the terrestrial nematodes of Victoria Land, Antarctica. ZooKeys 419:29–71

Aihara T (2001) *Iotonchium ungulatum* n. sp. (Nematoda: Iotonchiidae) from the oyster mushroom in Japan. Jpn J Nematol 31:1–11

Akiba M, Kanzaki N (2014) Soil nematode community in temperate beech forests and conifer plantations in Shirakami mountains. Nematol Res 44:60–61 (abstract)

Anand RL (2005) Association of a nematode *Ceratosolenus racemosa* gen. n. sp. n. (Cylindrocorpidae: Rhabditida Goodey, 1939), a wasp (*Ceratosolen* sp. n.) and fig *Ficus racemosa*. Uttar Pradesh J Zool 25:59–62

Banks N, Snyder TE (1920) A revision of the Nearctic termites with notes on biology and geographic distribution. US Natl Mus Bull 108:1–228

Bao Z, Ikunaga Y, Matsushita Y, Morimoto S, Takada-Hoshino Y, Okada H, Oba H, Takemoto S, Niwa S, Ohigashi K, Suzuki C, Nagaoka K, Takenaka M, Urashima Y, Sekiguchi H, Kushida A, Toyota K, Saito M, Tsushima S (2012) Combined analyses of bacterial, fungal and nematode communities in Andosolic agricultural soils in Japan. Microbes Environ 27:72–79

Bartholomaeus F, Davies KA, Ye W, Kanzaki N, Giblin-Davis RM (2009) *Schistonchus virens* sp. n. (Aphelenchoididae) and *Parasitodiplogaster australis* sp. n. (Diplogastridae) from *Ficus virens* (Moraceae) in Australia. Nematology 11:583–601

Blaxter ML, De Ley P, Garey JR, Liu LX, Scheldeman P, Vierstraete A, Vanfleteren JR, Mackey LY, Dorris M, Frisse LM, Vida JT, Thomas WK (1998) A molecular evolutionary framework for the phylum Nematoda. Nature (Lond) 392:71–75

Borgonie G, García-Moyano A, Litthauer D, Bert W, Bester A, Ev H, Möller C, Erasmus M, Onstott TC (2011) Nematoda from the terrestrial deep subsurface of South Africa. Nature (Lond) 474:79–82

Braasch H, Gu J, Burgermeister W, Brandstetter M, Metge K (2006) Description of *Ruehmaphelenchus asiaticus* sp. n. (Nematoda: Aphelenchoididae) and remarks on the genus *Ruehmaphelenchus*. J Nematode Morph Syst 9:39–48

Center BJ, Giblin-Davis RM, Herre EA, Chung-Schickler GC (1999) Histological comparisons of parasitism by *Schistonchus* spp. (Nemata: Aphelenchoididae) in neotropical *Ficus* spp. J Nematol 31:393–406

Cobb NA (1914) Nematodes and their relationships. USDA Yearb 1914:457–490

Creer S, Fonseca VG, Porazinska DL, Giblin-Davis RM, Sung W, Power DM, Packer M, Carvalho GR, Blaxter ML, Lambshead PJ, Thomas WK (2010) Ultrasequencing of the meiofaunal biosphere: practice, pitfalls and promises. Mol Ecol 19(S1):4–20

Crowe JH, Madin KAC (1975) Anhydrobiosis in nematodes: evaporative water loss and survival. J Exp Zool A 193:323–334

Davies KA, Ye W, Giblin-Davis RM, Thomas WK (2008) *Ficotylus congestae* gen. n., sp. n. (Anguinata), from *Ficus congesta* (Moraceae) sycones in Australia. Nematology 11:63–75

Davies KA, Ye W, Kanzaki N, Bartholomaeus F, Zeng Y, Giblin-Davis RM (2015) A review of the taxonomy, phylogeny, distribution and co-evolution of *Schistonchus* (Nematoda: Aphelenchoididae) and proposal of *Ficophagus* n. gen. and *Martininema* n. gen. Nematology 17:761–829

De Ley P, Blaxter ML (2002) Systematic position and phylogeny. In: Lee DL (ed) The biology of nematodes. Taylor & Francis, London, pp 1–30

Freckman DW, Virginia RA (1989) Plant-feeding nematodes in deep-rooting desert ecosystems. Ecology 70:1665–1678

Freckman DW, Virginia RA (1993) Extraction of nematodes from dry valley Antarctic soils. Pol Biol 13:483–487

Fürst von Lieven A (2003) The genus *Oigolaimella* Paramonov, 1952 (Nematoda: Diplogastridae) and description of *O. kruegeri* n. sp. and *O. ninae* n. sp. Nematology 5:583–600

Fürst von Lieven A, Sudhaus W (2008) Description of *Oigolaimella attenuata* n. sp. (Diplogastridae) associated with termites (*Reticulitermes*) and remarks on life cycle, giant spermatozoa, gut-inhabiting flagellates and other associates. Nematology 10:501–523

Gasparrini G (1864) Sulla maturazione e la qualità dei fiche dei contorni di Napoli. Atti Acad Pontaniana 9:99–118

Giblin RM, Kaya HK (1983) *Bursaphelenchus seani* n. sp. (Nematoda, Aphelenchoididae), a phoretic associate of *Anthophora bomboides stanfordiana* Cockerell, 1904 (Hymenoptera, Anthophoridae). Rev Nématol 6:39–50

Giblin RM, Kaya HK (1984) *Aduncospiculum halicti* n. gen., n. sp. (Diplogasterida: Diplogasteroididae), an associate of bees in the genus *Halictus* (Hymenoptera: Halictidae). Rev Nèmatol 7:189–197

Giblin RM, Swan J, Kaya HK (1984) *Bursaphelenchus kevini* n. sp. (Aphelenchoididae), an associate of bees of the genus *Halictus* (Hymenoptera: Halictidae). Rev Nèmatol 7:177–189

Giblin-Davis RM, Mundo-Ocampo M, Baldwin JG, Norden BB, Batra SWT (1993) Description of *Bursaphelenchus abruptus* n. sp. (Nemata: Aphelenchoididae), an associate of a digger bee. J Nematol 25:161–172

Giblin-Davis RM, Center BJ, Nadel H, Frank JH, Ramirez WB (1995) Nematodes associated with fig wasps, *Pegoscapus* spp. (Agaonidae), and the syconia of native Floridian figs (*Ficus* spp.). J Nematol 27:1–14

Giblin-Davis RM, Hazir S, Center BJ, Ye W, Keskin N, Thorp RW, Thomas WK (2005) *Bursaphelenchus anatolius* n. sp. (Nematoda: Parasitaphelenchidae), an associate of bees in the genus *Halictus*. J Nematol 37:336–342

Giblin-Davis RM, Erteld C, Kanzaki N, Zeng Y, Ye W, Center BJ (2010) *Ditylenchus halictus* n. sp. (Nematoda: Anguinidae), an associate of the sweat bee *Halictus sexcinctus* (Halictidae) from Germany. Nematology 12:891–904

Giblin-Davis RM, Kanzaki N, Davies KA (2013) Nematodes that ride insects: unforeseen consequences of arriving species. Fla Entomol 96:770–780

Giblin-Davis RM, Kanzaki N, Davies KA, Ye W, Zeng Y, Center BJ, Esquivel A, Powers TO (2014) *Ficotylus laselvae* n. sp. (Tylenchomorpha: Anguinidae) associated with *Ficus colubrinae* in Costa Rica. Nematology 16:1139–1151

Hazir C, Giblin-Davis RM, Keskin N, Ye W, Kanzaki N, Center BJ, Hazir S, Kaya HK, Thomas WK (2007) *Bursaphelenchus debrae* n. sp. (Nematoda: Parasitaphelenchidae), an associate of the bee *Halictus brunnescens* in Turkey. Nematology 9:777–789

Hazir C, Giblin-Davis RM, Keskin N, Ye W, Hazir S, Scheuhl E, Thomas WK (2010) Diversity and distribution of nematodes associated with wild bees in Turkey. Nematology 12:65–80

Hazir C, Kanzaki N, Gulcu B, Hazir S, Giblin-Davis RM (2015) Reverse taxonomy reveals *Pristionchus maupasi* (Diplogasterida: Diplogastridae) association with the soil-dwelling bee *Andrena optata* (Hymenoptera: Andrenidae) in Turkey. Fla Entomol 97:371–374

Herrmann M, Mayer WE, Sommer RJ (2006) Sex, bugs and Haldane's rule: the nematode genus *Pristionchus* in the United States. Front Zool 3:14

Holterman M, Wurff AVD, Elsen SVD, Megen HV, Bongers T, Holovachov O, Bakker J, Helder J (2006) Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution toward crown clades. Mol Biol Evol 23:1792–1800

Hunt DJ (1980) *Acugutturus parasiticus*, n. g., n. sp., a remarkable ectoparasitic aphelenchoid nematode from *Periplaneta americana* (L.), with proposal of Acugutturinae n. subf. Syst Parasitol 1:167–170

Hunt DJ (1998) *Rhigonema pilosum* sp. n. (Rhigonematida) parasitizing a member of the Xystodesmidae (Diplopoda: Polydesmida) from the Ryuku Islands, Japan. J Nematode Morph Syst 1:23–28

Inglis WG (1983) An outline classification of the Phylum Nematoda. Aust J Zool 31:243–255

Kaiser H (1987) Biology, ecology and development of the European parasitoid of yellowjackets *Pheromermis vesparum*, new species (Mermithidae, Nematoda). Zool Jb Syst Ökol Geogr 114:421–449

Kanzaki N (2006) Description of *Aphelenchoides xylocopae* n. sp. (Nematoda: Aphelenchoididae), the first observed association between nematodes and carpenter bees. Nematology 8:555–562

Kanzaki N (2016) Stomatal dimorphism of Neodiplogaster acaloleptae (Diplogastromorpha: Diplogastridae). PLoS One 11:e0155715

Kanzaki N, Futai K (2002) Phylogenetic analysis of the phoretic association between *Bursaphelenchus conicaudatus* (Nematoda: Aphelenchoididae) and *Psacothea hilaris* (Coleoptera: Cerambycidae). Nematology 4:759–771

Kanzaki N, Futai K (2003) Description and phylogeny of *Bursaphelenchus luxuriosae* n. sp. (Nematoda: Aphelenchoididae) isolated from *Acalolepta luxuriosa* (Coleoptera: Cerambycidae). Nematology 5:565–572

Kanzaki N, Futai K (2004) *Cylindrocorpus anoplophorae* n. sp. (Nematoda: Cylindrocorporidae) isolated from the white-spotted longicorn beetle, *Anoplophora malasiaca* (Coleoptera: Cerambycidae). Jpn J Nematol 34:11–19

Kanzaki N, Futai K (2005) Description of *Bursaphelenchus parvispicularis* n. sp. (Nematoda: Parasitaphelenchidae) isolated from a dead oak tree, *Quercus mongolica* var. *grosseserrata*. Nematology 7:751–759

Kanzaki N, Kosaka H (2009) Relationship between nematodes and bark and ambrosia beetles. J Jpn For Soc 91:446–460 [in Japanese with English summary]

Kanzaki N, Ide T (2016) Diplogasteroides luxuriosae n. sp. associated with Acalolepta luxuriosa (Cerambycidae) from Japan. Nematology 18:221–233

Kanzaki N, Tsuda K, Futai K (2000) Description of *Bursaphelenchus conicaudatus* n. sp. (Nematoda: Aphelenchoididae), isolated from the yellow-spotted longicorn beetle, *Psacothea hilaris* (Coleoptera: Cerambycidae) and fig trees, *Ficus carica*. Nematology 2:165–168

Kanzaki N, Minagawa N, Futai K (2002) Description of *Rhabdontolaimus psacotheae* n. sp. (Diplogasterida: Diplogasteroididae), isolated from the yellow-spotted longicorn beetle, *Psacothea hilaris* (Coleoptera: Cerambycidae) and fig tree, *Ficus carica*. Jpn J Nematol 32:7–12

Kanzaki N, Kobayashi M, Nozaki A, Futai K (2006) *Myctolaimus platypi* n. sp. (Nematoda: Cylindrocorporidae) isolated from the oak borer, *Platypus quercivorus* (Coleoptera: Platypodidae), the first observed association between nematodes and platypodid bark beetles. Nematology 8:717–725

Kanzaki N, Maehara N, Masuya H (2007a) *Bursaphelenchus clavicauda* n. sp. (Nematoda: Parasitaphelenchidae) isolated from *Cryphalus* sp. emerged from a dead *Castanopsis cuspidata* (Thunb.) Schottky var. *sieboldii* (Makino) Nakai in Ishigaki Island, Okinawa, Japan. Nematology 9:759–769

Kanzaki N, Kosaka H, Sayama K, Takahashi J, Makino S (2007b) *Sphaerularia vespae* sp. nov. (Nematoda, Tylenchomorpha, Sphaerularioidea), an endoparasite of the common hornet, *Vespa simillima* Smith (Insecta, Hymenoptera, Vespidae). Zool Sci 24:1134–1142

Kanzaki N, Aikawa T, Maehara N, Matsumoto K (2008a) *Bursaphelenchus doui* Braasch, Gu, Burgermeister & Zhang, 2005 (Aphelenchida: Parasitaphelenchidae), an associate of *Monochamus subfasciatus* Bates (Coleoptera: Cerambycidae) and *Pinus densiflora* Sieb. & Zucc. Nematology 9:69–78

Kanzaki N, Maehara N, Aikawa T, Togashi K (2008b) First report of parthenogenesis in the genus *Bursaphelenchus* Fuchs, 1937: a description of *Bursaphelenchus okinawaensis* sp. nov. isolated from *Monochamus maruokai* (Coleoptera: Cerambycidae). Zool Sci 25:861–873

Kanzaki N, Masuya H, Kubono T (2008c) Description of *Neodiplogaster crenatae* sp. n. and *N. acaloleptae* sp. n. (Nematoda: Diplogastridae) from Japan. Nematology 10:545–560

Kanzaki N, Giblin-Davis RM, Center BJ (2009a) Description of *Ektaphelenchoides spondylis* n. sp. (Nematoda: Ektaphelenchinae) isolated from *Spondylis buprestoides* (Coleoptera: Cerambycidae) in Japan. Nematology 11:181–188

Kanzaki N, Giblin-Davis RM, Zeng Y, Ye W, Center BJ, Thomas WK (2009b) *Acrostichus puri* n. sp. (Nematoda: Diplogastridae), a phoretic associate of *Augochlora pura mosieri* Cockerell (Hymenoptera: Halictidae). Nematology 12:49–64

Kanzaki N, Giblin-Davis RM, Davies K, Ye W, Center BJ, Thomas WK (2009c) *Teratodiplogaster fignewmani* gen. nov., sp. nov. (Nematoda: Diplogastridae) from the syconia of *Ficus racemosa* in Australia. Zool Sci 26:569–578

Kanzaki N, Giblin-Davis RM, Scheffrahn RH, Center BJ (2009d) *Poikilolaimus floridensis* n. sp. (Rhabditida: Rhabditidae) associated with termites (Kalotermitidae). Nematology 11:203–216

Kanzaki N, Giblin-Davis RM, Scheffrahn RH, Center BJ, Davies KA (2009e) *Pseudaphelenchus yukiae* n. gen., n. sp. (Tylenchina: Aphelenchidae) associated with *Cylindrotermes macrognathus* (Termitidae: Termitinae) in La Selva, Costa Rica. Nematology 11:869–881

Kanzaki N, Li H-F, Lan Y-C, Kosaka H, Giblin-Davis RM, Akiba M, Sahashi N, Ota Y (2009f) Termite-associated nematodes in the Asian subtropics. In: International nematology symposium of Russian Society of Nematologists "Nematodes in tropical ecosystems" [abstract]

Kanzaki N, Kawaguchi E, Aikawa T, Maehara N (2010a) On *Bursaphelenchus yongensis* Gu, Braasch, Burgermeister, Brandstetter & Zhang, 2006 in Japan. Nematology 12:803–806

Kanzaki N, Giblin-Davis RM, Wcislo WT, Zeng Y, Ye W, Center BJ, Esquivel A, Thomas KW (2010b) *Acrostichus megaloptae* n. sp. (Nematoda: Diplogastridae), a phoretic associate of *Megalopta* spp. (Hymenoptera: Halictidae) in Central America. Nematology 12:453–468

Kanzaki N, Giblin-Davis RM, Herre EA, Scheffrahn RH, Center BJ (2010c) *Pseudaphelenchus vindai* n. sp. (Tylenchomorpha: Aphelenchoididae) associated with termites (Termitidae) in Barro Colorado Island, Panama. Nematology 12:905–914

Kanzaki N, Maehara N, Aikawa T, Masuya H, Giblin-Davis RM (2011a) Description of *Bursaphelenchus kiyoharai* n. sp. (Tylenchina: Aphelenchoididae) with remarks on the taxonomic framework of the Parasitaphelenchinae Rühm, 1956 and Aphelenchoidinae Fuchs, 1937. Nematology 13:787–804

Kanzaki N, Taki H, Masuya H, Okabe K, Tanaka R, Abe F (2011b) Diversity of stag beetle-associated nematodes in Japan. Environ Entomol 40:281–288

Kanzaki N, Li H-F, Lan Y-C, Kosaka H, Giblin-Davis RM, Center BJ (2011c) *Poikilolaimus carsiops* n. sp. (Rhabditida: Rhabditidae) associated with *Neotermes koshunensis* (Kalotermitidae) in Kenting National Park, Taiwan. Nematology 13:155–164

Kanzaki N, Giblin-Davis RM, Scheffrahn RH, Taki H, Esquivel A, Davies KA, Herre EA (2012a) Reverse taxonomy for tying diversity of termite-associated nematodes: a practical application of methodology. PLoS ONE 7:e43865

Kanzaki N, Maehara N, Aikawa T, Matsumoto K (2012b) *Bursaphelenchus firmae* n. sp. isolated from *Monochamus grandis* (Coleoptera: Cerambycidae) isolated from *Abies firma* Sieb. & Zucc. Nematology 14:395–404

Kanzaki N, Taki H, Masuya H, Okabe K (2012c) *Bursaphelenchus tadamiensis* n. sp. (Nematoda: Aphelenchoididae), isolated from a stag beetle, *Dorcus striatipennis* (Coleoptera: Lucanidae), from Japan. Nematology 14:223–233

Kanzaki N, Ragsdale EJ, Herrmann M, Mayer WE, Tanaka R, Sommer R (2012d) *Parapristionchus giblindavisi* n. gen, n. sp. (Rhabditida: Diplogastridae) isolated from stag beetles (Coleoptera: Lucanidae) in Japan. Nematology 14:933–947

Kanzaki N, Giblin-Davis RM, Davies KA, Center BJ (2012e) *Teratodiplogaster martini* n. sp. and *Parasitodiplogaster doliostoma* n. sp. (Nematoda: Diplogastridae) from the syconia of *Ficus* species from Africa. Nematology 14:529–546

Kanzaki N, Tanaka R, Giblin-Davis RM, Ragsdale EJ, Nguyen CN, Li H-F, Lan Y-C (2012f) A preliminary survey of fig-associated nematodes in the Asian subtropics. J Nematol 44:470 [abstract]

Kanzaki N, Ragsdale EJ, Herrmann M, Mayer WE, Sommer RJ (2012g) Description of three nematode species from Japan, *Pristionchus exspectatus* n. sp., *P. arcanus* n. sp., and *P. japonicus* n. sp., which form a cryptic species complex including the model organism *P. pacificus* (Diplogastridae). Zool Sci 29:403–417

Kanzaki N, Tanaka R, Hirooka Y, Maehara N (2013a) Description of *Diplogasteroides andrassyi* n. sp., associated with *Monochamus grandis* and Pinaceae trees in Japan. J Nematode Morph Syst 16:35–47

Kanzaki N, Taki H, Masuya H, Okabe K, Chen C-Y (2013b) Description of *Ruehmaphelenchus formosanus* n. sp. (Tylenchina: Aphelenchoididae) isolated from *Euwallacea fornicates* from Taiwan. Nematology 15:895–906

Kanzaki N, Tanaka R, Ikeda H, Taki H, Sugiura S, Matsumoto K (2013c) Phylogenetic status of and insect parasitism in the subfamily Entaphelenchinae Nickle with description of *Peraphelenchus orientalis* n. sp. (Tylenchomorpha: Aphelenchoididae). J Parasitol 99:639–649

Kanzaki N, Ragsdale EJ, Herrmann M, Sommer RJ, Susoy V (2013d) Two androdioecious and one dioecious new species of *Pristionchus* (Nematoda: Diplogastridae): new reference points for the evolution of reproductive mode. J Nematol 45:172–194

Kanzaki N, Ragsdale EJ, Herrmann M, Röseler W, Sommer RJ (2013e) Two new species of *Pristionchus* (Nematoda: Diplogastridae) from Japan, including a new member of the *P. pacificus* species complex. Zool Sci 30:680–692

Kanzaki N, Ragsdale EJ, Susoy V, Sommer RJ (2014a) *Leptojacobus dorci* n. gen., n. sp. (Nematoda: Diplogastridae), an associate of *Dorcus* stag beetles (Coleoptera: Lucanidae). J Nematol 46:50–59

Kanzaki N, Tanaka R, Giblin-Davis RM, Davies KA (2014b) New plant-parasitic nematode from the mostly mycophagous genus *Bursaphelenchus* discovered inside figs in Japan. PLoS ONE 9: e99241

Kanzaki N, Giblin-Davis RM, Davies KA (2014c) Diversity of fig-associated nematodes as a model system for studying biogeography, host switching and colonization of new habitats. In: 6th international congress of nematology abstracts, p 44

Kanzaki N, Woodruff GC, Tanaka R (2014d) *Teratodiplogaster variegatae* n. sp. isolated from the syconia of *Ficus variegata* Blume on Ishigaki Island, Okinawa, Japan. Nematology 16:1153–1166

Kanzaki N, Li H-F, Lan Y-C, Giblin-Davis RM (2014e) Description of two *Pseudaphelenchus* species (Tylenchomorpha: Aphelenchoididae) associated with Asian termites and proposal of new subfamily Tylaphelenchinae n. subfam. Nematology 16:963–978

Kanzaki N, Woodruff GC, Akiba M, Maehara N (2015a) *Diplogasteroides asiaticus* n. sp. is associated with *Monochamus alternatus* in Japan. J Nematol 47:105–115

Kanzaki N, Giblin-Davis RM, Gonzalez R, Duncan R, Carrillo D (2015b) Description of *Ruehmaphelenchus juliae* n. sp. (Tylenchina: Aphelenchoididae) isolated from an ambrosia beetle, *Xylosandrus crassiusculus* (Motschulsky), from South Florida. Nematology 17:639–653

Kanzaki N, Okabe K, Kobori Y (2015c) *Bursaphelenchus sakishimanus* n. sp. (Tylenchomorpha: Aphelenchoididae) isolated from a stag beetle, *Dorcus titanus sakishimanus* Nomura (Lucanidae), on Ishigaki Island in Japan. Nematology 17:531–542

Kanzaki N, Giblin-Davis RM, Ragsdale EJ (2015d) *Allodiplogaster josephi* n. sp. and *A. seani* n. sp. (Nematoda: Diplogastridae), associates of soil-dwelling bees in the eastern USA. Nematology 17:831–863

Kanzaki N, Giblin-Davis RM, Gonzalez R, Trujillo Y, Hajek AE (2016a) Tylenchid entomoparasites isolated from Spondylis buprestoides (L.) and Asemum striatum (L) (Coleoptera: Cerambycidae). Nematology 18:775–780

Kanzaki N, Okabe K, Kajimura H (2016b) Rhabditidoides aegus n. sp., an associate of stag beetles and sap flow in Japan. Nematology 18:195–208

Kanzaki N, Sakamoto H, Maehara N (2016c) Diplogasteroides nix n. sp. (Nematoda: Diplogastridae), a cryptic species related to D. andrassyi, isolated from Monochamus urussovii (Coleoptera: Cerambycidae) from Hokkaido, Japan, with remarks on the body surface structures. Nematology 18:753–773

Körner H (1954) Die Nematodenfauna des vergehenden Holzes und ihre Beziehungen zu den Insekten. Zool Jb 82:245–353

Kosaka H, Ogura N (1993) *Contortylenchus genitalicola* n. sp. (Tylenchida:Allantonematidae) from the Japanese pine sawyer, *Monochamus alternatus* (Coleoptera: Cerambycidae). Appl Entomol Zool 28:423–432

Kosaka H, Sayama K, Kanzaki N, Makino S, Okabe K (2012) Parasites of the introduced bumblebee, *Bombus terrestris*, naturalized in Hokkaido, northern Japan. Glob Environ Res 17:135–141 [in Japanese with English summary]

Kubo R, Ugajin A, Ono M (2016) Molecular phylogenetic analysis of mermithid nematodes (Mermithida: Mermithidae) discovered from Japanese bumblebee (Hymenoptera: Bombinae) and behavioral observation of an infected bumblebee. Appl Entomol Zool 51:549–554. doi:10.1007/s13355-016-0430-7

Kuwata R, Shigematsu M, Yoshiga T, Yoshida M, Kondo E (2006) Phylogenetic analyses of Japanese steinernematid nematodes and their associating *Xenorhabdus* bacteria. Jpn J Nematol 36:75–85

Leidy J (1877) On intestinal parasites of *Termes flavipes*. Proc Acad Nat Sci Phila 29:146–149

Maggenti AR (1983) Nematode higher classification as influenced by species and family concepts. In: Stone AR, Platt HM, Khalil LF (eds) Concepts in nematode systematics. Academic, London, pp 25–40

Maggenti AR (1991) Nemata: higher classification. In: Nickle WR (ed) Manual of agricultural nematology. Dekker, New York, pp 147–187

Mamiya Y (1988) *Steinernema kushidai* n. sp. (Nematoda: Steinernematidae) associated with scarabaeid beetle larvae from Shizuoka, Japan. Appl Entomol Zool 23:313–320

Mamiya Y, Enda N (1979) *Bursaphelenchus mucronatus* n. sp. (Nematoda: Aphelenchoididae) from pine wood and its biology and pathogenicity to pine trees. Nematologica 25:353–361

Mamiya Y, Kiyohara T (1972) Description of *Bursaphelenchus lignicolus* n. sp. (Nematoda: Aphelenchoididae) from pine wood and histopathology of nematode-infested trees. Nematologica 18:120–124

Martin GC, Owen AC, Way JI (1973) Nematodes, figs and wasps. J Nematol 5:77–78

Massey CL (1971) Two new genera of nematodes parasitic in the eastern subterranean termites *Reticulitermes flavipes*. J Invertebr Pathol 17:238–242

Massey CL (1974) Biology and taxonomy of nematode parasites and associates of bark beetles in the United States, Agriculture handbook no. 446. USDA Forest Service, Washington, DC

Megan HV, Elsen SVD, Holterman M, Karssen G, Mooyman P, Bongers T, Holovachov O, Bakker J, Helder J (2009) A phylogenetic tree of nematodes based on about 1200 full-length small subunit ribosomal DNA sequences. Nematology 11:927–950

Morise H, Miyazaki E, Yoshimitsu S, Eki T (2012) Profiling nematode communities in unmanaged flowerbed and agricultural field soils in Japan by DNA barcode sequencing. PLoS ONE 7: e51785

Nobuchi A (1977) Platypodidae found in imported tropical timbers from South East Asia and Others (Coleoptera). Bull Gov For Exp Sta 296:101–155 [in Japanese with English summary]

Ogata K, Tanaka I, Ogawa T (1975) Studies on establishing factors of domiciliary cockroaches. 1. Field surveys of the distribution of domiciliary cockroaches in Tokyo and Kawasaki. Jpn J Sanit Zool 26:241–245

Okada H, Ohba H (2008) Comparison of nematode community similarities assessed by polymerase chain reaction-denaturing gradient gel electrophoresis (DGGE) and by morphological identification. Nematology 10:689–700

Okumura E, Tanaka R, Yoshiga T (2013a) Species-specific recognition of the carrier insect by dauer larvae of the nematode *Caenorhabditis japonica*. J Exp Biol 216:568–572

Okumura E, Tanaka R, Yoshiga T (2013b) Negative gravitactic behavior of *Caenorhabditis japonica* dauer larvae. J Exp Biol 216:1470–1474

Ozawa S, Vicente CSL, Sato K, Yoshiga T, Kanzaki N, Hasegawa K (2014) First report of the nematode *Leidynema appendiculata* from *Periplaneta fuliginosa*. Acta Parasitol 59:219–228

Pemberton CE (1928) Nematode associated with termites in Hawaii, Borneo and Celebes. Proc Hawai Entomol Soc 7:148–150

Phan KL, Takemoto S, Futai K (2006) *Steinernema ashiuense* sp. n. (Nematoda: Steinernematidae), a new entomopathogenic nematode from Japan. Nematology 8:681–690

Pinto TK, Austen MCV, Warwick RM, Somerfield PJ, Esteves AM, Castro FJV, Fonseca-Genevois VG, Santos PJP (2013) Nematode diversity in different microhabitats in a mangrove region. Mar Ecol 34:257–268

Poinar GO (1975) Entomogenous nematodes: a manual and host list of insect-nematode associations. Brill, Leiden

Poinar GO (1979) *Parasitodiplogaster sycophilon* gen. n., sp. n. (Diplogasteridae: Nematoda), a parasite of *Elisabethiella stuchenbergi* Grandi (Agaonidae: Hymenoptera) in Rhodesia. Proc Kon Ned Akad Wetensch C Amsterdam 82:375–381

Poinar GO (1983) The natural history of nematodes. Prentice-Hall, Englewood Cliffs

Poinar GO, Herre EA (1991) Speciation and adaptive radiation in the fig wasp nematode, *Parasitodiplogaster* in Panama. Rev Nématol 14:361–374

Porazinska DL, Giblin-Davis RM, Farmerie W, Powers TO, Kanzaki N, Faller L, Morris K, Sung W, Thomas WK (2009) Evaluating high throughput sequencing as a method for metagenomic analysis of nematode diversity. Mol Ecol Res 9:1439–1450

Powers TO, Neher DA, Mullin P, Esquivel A, Giblin-Davis RM, Kanzaki N, Stock SP, Mora MM, Uribe-Lorio L (2009) Tropical nematode diversity: vertical stratification of nematode communities in a Costa Rican humid lowland rainforest. Mol Ecol 18:985–996

Ragsdale EJ, Müller MR, Rödelsperger C, Sommer RJ (2013a) A developmental switch coupled to the evolution of plasticity acts through a sulfatase. Cell 155:922–933

Ragsdale EJ, Kanzaki N, Röseler W, Herrmann M, Sommer RJ (2013b) Three new species of *Pristionchus* (Nematoda: Diplogastridae) show morphological divergence through evolutionary intermediates of a novel feeding polymorphism. Zool J Linn Soc 168:671–698

Ragsdale EJ, Kanzaki N, Herrmann M (2015) Taxonomy and natural history: the genus *Pristionchus*. In: Sommer RJ, Hunt DJ, Perry RN (eds) *Pristionchus pacificus*: a nematode model for comparative and evolutionary biology, vol 11, Nematology Monographs and Perspectives. Brill, Leiden, pp 77–120

Rödelsperger C, Neher RA, Weller A, Eberhardt G, Witte H, Mayer WE, Dieterich C, Sommer RJ (2014) Characterization of genetic diversity in the nematode *Pristionchus pacificus* from population-scale resequencing data. Genetics 196:1153–1165

Rosenberg JS (2003) Of ants and earth; E.O. Wilson's view of life takes in all things small and great. Harvard Mag March-April:36–41

Rühm W (1956) Die Nematoden der Ipiden. Parasitologische Schriftenreihe 6:1–435

Sapkota R, Nicolaisen M (2015) High-throughput sequencing of nematode communities from total soil DNA extractions. BMC Ecol 15:3

Serobyan V, Ragsdale EJ, Sommer RJ (2014) Adaptive value of a predatory mouth-form in a dimorphic nematode. Proc R Soc B 281:20141334

Shimizu A, Tanaka R, Akiba M, Masuya H, Iwata R, Fukuda K, Kanzaki N (2013) Nematodes associated with *Dryocoetes uniseriatus* Eggers (Coleoptera: Scolytidae). Environ Entomol 42:79–88

Shinya R, Hasegawa K, Chen A, Kanzaki N, Sternberg PW (2014) Evidence of hermaphroditism and sex ratio distortion in the fungal feeding nematode *Bursaphelenchus okinawaensis*. G3 Genes Genomes Genet 4:1907–1917

Sommer RJ (2009) The future of evo-devo: model systems and evolutionary theory. Nat Rev Genet 10:416–422

Southey JF (ed) (1986) Laboratory methods for work with plant and soil nematodes, vol 2, Technical bulletin. Her Majesty's Stationery Office, London

Sriwati R, Afriyani JJ, Takeuchi Y, Tanaka R, Kanzaki N (2013) Nematodes associated with syconia of Ficus racemosa. Nematol Res 43:44–45 [abstract]

Sudhaus W, Koch C (2004) The new nematode species *Poikilolaimus ernstmyri* sp. n. associated with termites, a discussion on the phylogeny of *Poikilolaimus* (Rhabditida). Russ J Nematol 12:143–156

Susoy V, Herrmann M (2014) Preferential host switching and codivergence shaped radiation of bark beetle symbionts, nematodes of *Micoletzkya* (Nematoda: Diplogastridae). J Evol Biol 27:889–898

Susoy V, Ragsdale EJ, Kanzaki N, Sommer RJ (2015) Rapid diversification associated with a macroevolutionary pulse of developmental plasticity. eLIFE 4:e05463

Tanaka R, Okumura E, Kanzaki N, Yoshiga T (2012) Low survivorship of dauer larva in the nematode *Caenorhabditis japonica*, a potential comparative system for a model organism, *C. elegans*. Exp Gerontol 47:388–393

Tanaka R, Hino A, Tsai IJ, Palomares-Rius JE, Yoshida A, Ogura Y, Hayashi T, Maruyama H, Kikuchi T (2014a) Assessment of helminth biodiversity in wild rats using 18S rDNA based metagenomics. PLoS ONE 9:e110769

Tanaka SE, Tanaka R, Akiba M, Aikawa T, Maehara N, Takeuchi Y, Kanzaki N (2014b) *Bursaphelenchus niphades* n. sp. (Tylenchina: Aphelenchoididae) amensally associated with *Niphades variegatus* (Roelofs) (Coleoptera: Curculionidae). Nematology 16:259–281

Tsuda K, Futai K (1999) *Iotonchium cateniforme* n. sp. (Tylenchida: Iotonchiidae) from fruiting bodies of *Cortinarius* spp. and its life cycle. Jpn J Nematol 29:24–31

Tsuda K, Futai K (2005) Description of two new species of *Iotonchium* Cobb, 1920 (Tylenchida: Iotonchiidae) from Japan. Nematology 7:789–801

Tsuda K, Kosaka H, Futai K (1996) The tripartite relationship in gill-knot disease of the oyster mushroom, *Pleurotus ostreatus* (Jacq.: Fr.) Kummer. Can J Zool 74:1402–1408

Vandegehuchte ML, Sylvain ZA, Reichmann LG, de Tomasel CM, Nielsen UN, Wall DH, Sala OE (2015) Responses of a desert nematode community to changes in water availability. Ecosphere 6:art44

Vovlas N, Larizza A (1996) Relationship of *Schistonchus caprifici* (Aphelenchoididae) with fig inflorescences, the fig pollinator *Blastophaga psenes*, and its cleptoparasite *Philotrypesis caricae*. Fundam Appl Nematol 19:443–448

Wachek F (1955) Die entoparasitischen Tylenchiden. Parasitologische Schrift 3:1–119

Weller AM, Mayer WE, Rae R, Sommer RJ (2010) Quantitative assessment of the nematode fauna present on *Geotrupes* dung beetles reveals species-rich communities with a heterogeneous distribution. J Parasitol 96:525–531

Wöhr M, Greeff JM, Kanzaki N, Giblin-Davis RM (2015) *Parasitodiplogaster salicifoliae* n. sp. (Nematoda: Diplogastrina) from *Ficus ingens* and *F. salicifolia* in South Africa. Nematology 17:301–311

Yeates GW, Bongers T, De Goede RGM, Freckman DW, Georgieva SS (1993) Feeding habits in soil nematode families and genera—an outline for soil ecologists. J Nematol 25:315–331

Yoshida M (2004) *Steinernema litorale* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Japan. Nematology 6:819–838

Yoshida M, Reid AP, Briscoe BR, Hominick WM (1998) Survey of entomopathogenic nematodes (Rhabditida: Steinernematidae and Hererorhabditidae) in Japan. Fundam Appl Nematol 21:185–198

Zrzavý J, Mihulka S, Kepka P, Bezděk A, Tietz D (1998) Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. Cladistics 14:249–285

Chapter 12
Diversity of Leeches from Japan: Recent Progress in Macrophagous and Blood-Feeding Taxa

Takafumi Nakano

Abstract The species diversity of the leeches from Japan and recent progress in taxonomic and molecular phylogenetic studies on macrophagous and blood-feeding taxa are reviewed. At present, 64 species are known in Japan, which are classified into 38 genera in 9 families. Recent taxonomic and molecular phylogenetic analyses have revealed that the terrestrial macrophagous genus *Orobdella* is the most diverse taxon among the genera distributed in Japan. The phylogenetic relationships and geographic distributions of *Orobdella* species suggest that this genus has been highly influenced by geological events and geographic boundaries. In contrast, phylogenetic relationships between blood-feeding species of the genus *Haemadipsa* show that Japanese species do not form a monophyletic group, suggesting multiple origins of the species. Phylogenetic relationships of *Haemadipsa rjukjuana* shed light on the incongruence between its genetic structure and geographic distances. The results indicate that blood-feeding leeches have been dispersed via long-distance migrants. The low genetic diversity of freshwater predatory *Mimobdella* in the Ryukyu Islands, as well as the presence of the freshwater-introduced species in Japan, indicate the possibility of the influence of human activities on the present distribution of freshwater species.

Keywords Hirudinida • Species diversity • Japan • Phylogeny • *Orobdella* • *Haemadipsa* • *Mimobdella*

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12.1 Introduction

12.1.1 Leech Morphology: Somite Annulation and Digestive System

Leeches (Hirudinida) are a well-known achaetous and hermaphrodite annelid taxon of predatory worms. Hirudinida possess two suckers: an oral sucker at the anterior end of the body and a caudal sucker at the posterior end. Bearing these two suckers is the most distinguishable morphological characteristic of Hirudinida from other annelid taxa. Differing from polychaete and oligochaete taxa, the number of body somites is constant in members of Hirudinida. A leech body is composed of 34 somites, and its caudal sucker comprises the 27th–34th somites. The body somite surface bears several transversal furrows, and thus each body somite appears externally to consist of several rings (annuli). The number of annuli in the middle body somites is generally an important diagnostic characteristic of leech taxa.

Although all leeches are predaceous taxa, their feeding habits vary: liquidosomatophagous, feeding on invertebrate fluids; haematophagous, blood-feeder; and macrophagous, feeding on invertebrates. Thus, the digestive system is an important organ within Hirudinida. The digestive tract consists of a mouth opening in the oral sucker, pharynx, esophagus, crop, intestine, and rectum. The anus opens on the dorsal surface, anterior to the caudal sucker. Whereas some taxa possess a proboscis in the pharynx, well-known blood-feeders, represented by the medicinal leech, bear muscularized jaws and teeth on each jaw instead of a proboscis. Some macrophagous leech taxa completely lack a proboscis or dentate jaws, but possess a developed muscularized pharynx.

12.1.2 Phylogenetic Position of Hirudinida Within Annelida

Molecular phylogenetic studies from the 1990s confirmed that Hirudinida is a member of Clitellata, which consists mainly of oligochaete worms (Rousset et al. 2006). In addition to Hirudinida, two other parasitic taxa, Acanthobdellida and Branchiobdellida, have been classified under Clitellata. Acanthobdellida is a fish parasite distributed in the boreal region (Sawyer 1986). This taxon possesses transitional morphological characteristics between those of leeches and oligochaetes. Branchiobdellida is an ectoparasite of freshwater crustaceans and inhabits the northern hemisphere (Sawyer 1986). This taxon bears a caudal sucker, but lacks chaetae and an oral sucker. A recent molecular phylogenetic study revealed that Hirudinida, Acanthobdellida, and Branchiobdellida are monophyletic, and that the clade is a sister group to the aquatic lumbriculid oligochaetes (Siddall et al. 2001). In terms of morphological characteristics, a clitellum, a saddle-like structure, can be clearly defined as the synapomorphy of Clitellata, including Hirudinida, Acanthobdelida, and Branchiobdellida.

12.1.3 Classification and Phylogeny of Higher-Level Leech Taxa

The current classification system of Hirudinida was established by Sawyer (1986). Traditionally, Hirudinida has been classified into two orders (Fig. 12.1): Rhynchobdellida and Arhychobdellida. Rhynchobdellida, which possesses a proboscis, contains three families: freshwater Glossiphoniidae, marine and freshwater Piscicolidae (fish-parasite), and marine and freshwater Ozobranchidae (chelonian-ectoparasite). The other order is composed of leeches lacking a proboscis. Arhynchobdellida has been divided into two suborders: Hirudiniformes and Erpobdelliformes. Hirudiniformes contains haematophagous leeches and predatory species, whereas members of Erpobdelliformes are predatory taxa. Sawyer (1986) characterized these two suborders by their pharyngeal characteristics and feeding preferences. The muscular ridges of the hirudiniform pharynx reach straight to the crop (euthylaematous pharynx). However, those of the erpobdelliform pharynx reach to the crop with a rotation of 60° to the right (strepsilaematous pharynx).

Recently, phylogenetic relationships among the higher-level taxa have been studied based on morphological (Siddall and Burreson 1995), molecular (Siddall and Burreson 1998), and both morphological and DNA data (Apakupakul

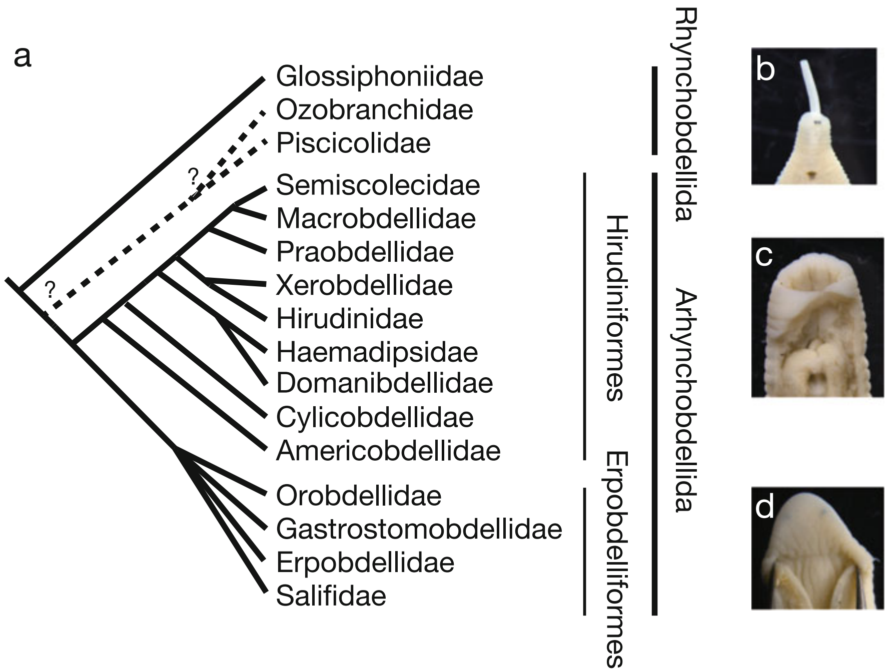

Fig. 12.1 Phylogenies and pharyngeal characters of families in Hirudinida. (**a**) Phylogenetic relationships of families and their classification. (**b**) A proboscis of Glossiphoniidae. (**c**) Three jaws in the oral cavity of Hirudinidae. (**d**) A jaw-less pharynx of Orobdellidae

et al. 1999). Apakupakul et al. (1999) revealed that Rhynchobdellida is a paraphyletic taxon; specifically, Glossiphoniidae is a sister group to the clade consisting of the clade of Piscicolidae and Ozobranchidae, and Arhynchobdellida. However, morphology-based phylogenetic analyses still support the monophyly of three rhynchobdellid families (Bielecki et al. 2014). The phylogenetic position of the family Ozobranchidae has not yet been settled. Several studies have shown that this family is monophyletic with Piscicolidae (Apakupakul et al. 1999; Siddall and Burreson 1998). However, phylogenetic analyses of piscicolid leeches have failed to support their monophyly (Utevsky and Trontelj 2004; Utevsky et al. 2007).

Although the monophyly of Arhynchobdellida has been well supported (Bielecki et al. 2014; Apakupakul et al. 1999; Borda and Siddall 2004), the family-level classification of arhynchobdellid leeches has been revamped drastically. Borda et al. (2008) and Borda and Siddall (2011) accomplished phylogenetic analyses of terrestrial blood-feeders of Hiruniformes, as represented by Haemadipsidae, and revised their family-level classification. Additionally, two families, Hirudinida and Haemopidae, were put together into one family by Phillips and Siddall (2009). Molecular phylogenetic studies also revealed that Hirudiniformes could not be diagnosed by its possession of a euthylaematous pharynx (Oceguera-Figueroa et al. 2011; Nakano et al. 2012). These studies revealed that Asian terrestrial macrophagous taxa bearing a euthylaematous pharynx belong to Erpobdelliformes. Although Sawyer's classification is basically followed in this chapter, the classification of Arhynchobdellida taxa is based on the recent molecular phylogenetic studies (Oceguera-Figueroa et al. 2011; Nakano et al. 2012; Phillips and Siddall 2009; Phillips et al. 2010; Borda et al. 2008; Borda and Siddall 2011).

12.2 History of Taxonomic Studies on Leeches in Japan

12.2.1 Before 1900: Charles O. Whitman and Raphaël Blanchard

Nakano and Itoh (2011) briefly reviewed the dawn of leech taxonomic studies in Japan. Charles O. Whitman was the first researcher to perform intensive taxonomic studies on Japanese leeches. During the period when Whitman was employed as a professor of zoology at the College of Science, the University of Tokyo in 1879–1881, he collected terrestrial, freshwater, and marine leech species inhabiting Japan. After he returned to the United States (USA), he wrote one paper entitled "The Leeches of Japan" (Whitman 1886). Whitman described two haematophagous species, *Hirudo nipponia* Whitman, 1886 and *Haemadipsa japonica* Whitman, 1886, the best known blood-feeders in Japan, as well as three predaceous species, *Whitmania acranulata* (Whitman, 1886), *W. edentula* (Whitman, 1886), and

W. pigra (Whitman, 1884), belonging to the family Hirudinidae (Whitman 1884, 1886).

In 1897, the French parasitologist Raphaël Blanchard described a new genus for a new species, *Mimobdella japonica* Blanchard, 1897b, based on a specimen collected by Philipp Franz von Siebold (Blanchard 1897b). Its type locality is stated only as Japan on its original label (Nakano 2011a). Blanchard also mentioned a specimen collected from Nikko, Japan, by Franz Martin Hilgendorf, along with the Siebold's material.

12.2.2 Asajiro Oka, the Great Japanese Researcher in Leech Taxonomy

The first Japanese leech taxonomist was Asajiro Oka. Although he specialized not only in leeches but also in other invertebrate taxa, he described 41 nominal species group taxa of Hirudinida during 1895–1935 (not 33 species as in Sket and Trontelj 2008). In the beginning of his career as a leech taxonomist, he released two reports on Japanese leeches (Oka 1895a, b). In Oka (1895b), he established the new genus *Orobdella* Oka, 1895b for the Japanese terrestrial macrophagous leeches along with a description of 3 new species under this genus. In 1910, he provided a "key" for Japanese leeches, which was written in Japanese, and described 14 new species from Japan (Oka 1910a). In addition to those 14 new species, he also described three new varieties of hirudiniform species. In the same year, he released a "synopsis" of Japanese leeches, written in German, and added one new variety of haemadipsid species in Taiwan. As mentioned by Nakano and Sung (2014), those names, stated as varieties, had a subspecific rank from the original publications according to the International Code of Zoological Nomenclature.

In 1917, he established a new glossiphoniid genus, *Ancyrobdella* Oka, 1917, along with a new *Ancyrobdella* species based on specimens collected from Lake Biwa (Oka 1917). In 1923, he used the terms "euthylaematous" and "strepsilaematous," based on the results of his examination of the pharynx of Japanese erpobdelliform leeches (Oka 1923). In 1925 and 1926, he published three taxonomic papers entitled "Notices sur les Hirudinées d'Extreme Orient" (Oka 1925a, b, 1926). After 1926, almost all his works were published in the *Proceedings of the Imperial Academy* (e.g., Oka 1927, 1928, 1929). In those brief taxonomic reports, he provided mainly detailed external morphologies of the species. He also described new species group taxa from Japan and adjacent regions. In 1935, he enumerated 53 species group taxon names in a brief list of Japanese leeches based on his previous taxonomic studies (Oka 1935).

12.2.3 From Asajiro Oka to the Present

Taxonomic studies on Japanese leeches diminished after Oka. Before 2000, foreign researchers contributed to knowledge on Japanese leeches: Pawłowski (1962) described a new subspecies of the family Erpobdellidae; Keegan et al. (1968) reported hirudiniform blood-sucking species; Richardson (1971, 1975) studied *Orobdella* species in Japan and described one new species from Hokkaido; and Nesemann (1997, 1995) studied erpobdelliform leeches and *Ancyrobdella* in Japan. Recent taxonomic studies on piscicolid species from Japanese coastal waters have also been carried out by foreign taxonomists (Burreson and Kearn 2000; Furiness et al. 2007; Utevsky and Chernyshev 2013).

Since the beginning of the twenty-first century, however, taxonomic studies on Japanese leeches have again been conducted by Japanese researchers. Itoh (2001) validated morphological variation of a Japanese glossiphoniid species. Since 2010, the taxonomic status of the Japanese macrophagous erpobdelliform species has been revisited serially (Nakano 2010, 2011a, b, c, 2012a, b, c, 2013, 2014).

12.3 Overview of the Species Diversity of Japanese Hirudinida

According to Sket and Trontelj (2008), approximately 680 Hirudinida species are known worldwide and are classified into 90 genera. However, it was stated that 185 species had been recorded in the Palearctic region including the main Japanese islands.

The precise number of Japanese leech species has not yet been determined. Ohno (2001) listed 56 species group taxa from Japan. In his list, 14 glossiphoniid, 17 piscicolid, 3 ozobranchid, 11 hirudiniform, and 11 erpobdelliform species were indicated. Nagasawa et al. (2008) provided a well-documented synopsis of Piscicolidae and Ozobranchidae distributed in Japanese lands and surrounding waters and showed 17 piscicolid and 3 ozobranchid known species. Additionally, Itoh (2010) reported the number of freshwater species from Japan: Glossiphoniidae, 14 species; Piscicolidae, 4 species; Ozobranchidae, 1 species; Hirudiniformes, 7 species; Erpobdelliformes, 8 species.

Based on the foregoing and additional records of species occurring in Japan and surrounding waters (Nagasawa and Uyeno 2009; Utevsky and Chernyshev 2013; Nakano 2010, 2011b, c, 2012a, b, 2014; Yamauchi et al. 2013), Table 12.1 shows the numbers of genera and species for each family known in Japan. Recent systematic and phylogenetic studies of leeches shed light on taxonomic issues related to Japanese leeches. Those findings are addressed here for each higher-level taxon.

Table 12.1 Family-level number of leech genera and species group taxa known in Japan

Family	Genus	Species group
Rhynchobdellida		
Glossiphoniidae	11	15
Ozobranchidae	1	3
Piscicolidae	16	19
Arhynchobdellida		
Hirudiniformes		
Haemadipsidae	1	3
Hirudinidae	2	5
Praobdellidae	2	2
Erpobdelliformes		
Erpobdellidae	1	2
Orobdellidae	1	11
Salifidae	3	4

12.3.1 Glossiphoniidae

According to present distributional records, the genus *Ancyrobdella* is considered endemic to Japan. This genus includes two species: *Ancyrobdella biwae* Oka, 1917, known only in Lake Biwa, and *Ancyrobdella smaragdina* (Oka, 1910a), known in the Kinki region of Honshu and Shikoku (Nesemann 1997). However, their phylogenetic position within Glossiphoniidae remains uncertain, despite the fact that only *Ancyrobdella* possesses hook-like structures at the anterior end of its proboscis.

Four species, *Glossiphonia complanata* (Linnaeus, 1758), *Hemiclepsis marginata* (Müller, 1774), *Helobdella stagnalis* (Linnaeus, 1758), and *Theromyzon tessulatum* (Müller, 1774), are distributed throughout the Palearctic region including Japan. Itoh (2001) suggested that the Japanese *H. stagnalis* could be separated into several species. Lai et al. (2009) revisited the taxonomic account of species of this genus in Taiwan and described two new species. Thus, the taxonomic status of the Japanese populations of these cosmopolitan species should be clarified.

Itoh (2010) listed two amphibian-parasite species of the genus *Oligobdella* Moore, 1918 whose mid-body somites are biannulate (two annuli). However, Siddall et al. (2005) synonymized *Oligobdella* with the other glossiphoniid genus in accordance with its molecular phylogenetic position. Moreover, Oceguera-Figueroa (2012) showed that biannulate mid-body somite annulation had evolved in parallel within Glossiphoniidae. Thus, the generic position of the Japanese *Oligobdella* species should be reinvestigated by molecular phylogenetic analyses.

12.3.2 Piscicolidae and Ozobranchidae

The freshwater piscicolid *Limmotrachelobdella sinensis* (Blanchard, 1896) has been reported recently from the Kinki region, western Honshu (Nagasawa et al. 2009; Nagasawa and Tanaka 2012; Ogawa et al. 2007). These studies suggested that this species may have been introduced to Japan in recent years. One freshwater ozobranchid species, *Ozobranchus jantseanus* Oka, 1912, for which the type locality is Wuchang District, China, has been recorded in Honshu and Shikoku (Yamauchi and Suzuki 2008). Yamauchi and Suzuki (2008) and Yamauchi et al. (2012) stated that the tortoises *Mauremys reevesii* and *M. japonica* were considered as the main hosts for this species. Suzuki et al. (2011) indicated the possibility that *M. reevesii* had been introduced artificially to Japan from adjacent countries in recent years. Because Oka (1935) did not include *O. jantseanus* in the Japanese leech list, it is also possible that this species artificially invaded Japan with its host(s). Further molecular phylogenetic studies are necessary to determine whether this species is an introduced species.

12.3.3 Hirudiniformes

The Hirudinidae inhabiting Japan are classified into two genera: blood-feeding *Hirudo* Linnaeus, 1758 and predaceous *Whitmania* Blanchard, 1888. Phillips and Siddall (2009) revealed that *Hirudo nipponia* is a sister group to *Whitmania* species based on molecular phylogenetic analyses. Additionally, Kovalenko and Utevsky (2015) stated that the size and number of teeth of *H. nipponia* is not similar to those of the European *Hirudo* species, although other morphological characteristics of *H. nipponia* are similar to the European species. The taxonomic position of *H. nipponia* thus remains to be clarified.

12.3.4 Erpobdelliformes

Itoh (2010) indicated that *Erpobdella octoculata* (Linnaeus, 1758) and *E. lineata* (Müller, 1774) were known in Japan. According to the brief review by Nesemann (1995), however, these two species inhabiting Japan should be considered as *E. japonica* Pawłowski, 1962, once described as a subspecies of *E. octoculata*. Previous molecular phylogenetic studies also confirmed that the subspecies could be treated as a distinct species from *E. octoculata* (Siddall 2002; Oceguera-Figueroa et al. 2011). Additionally, Ohno (2001) counted *Trocheta subviridis* (Dutrochet, 1817) as a member of Erpobdellidae distributed in Japan. However, Nakano and Itoh (2011) indicated that the past records of this species in Japan might be based on the misidentification of the salifid species.

The salifid *Barbronia weberi formosana* (Oka, 1929) has been recorded in Japan. According to molecular data, Oceguera-Figueroa et al. (2011) mentioned that *B. weberi* (Blanchard, 1897a) was unquestionably an invasive species, and most names for species group taxa of this genus should be synonymized with the species name *weberi*. The taxonomic status of *B. w. formosana* inhabiting Japan should thus be revisited.

12.3.5 Recent Progress in Understanding Japanese Leech Diversity

On the whole, the species diversity of leeches inhabiting Japan remains far from being determined. Because of a general lack of molecular data on leeches known in Japan, even the generic positions of many remain uncertain. In recent years, however, taxonomic and molecular phylogenetic studies have been conducted on some taxa distributed in Japan. Although the number of such studies is still limited, they have revealed noteworthy cryptic species diversity, genetic divergence, and phylogenetic relationships of Japanese leeches. In the following sections, these recent studies are reviewed: the high diversity and phylogenetic relationships of the terrestrial macrophagous genus *Orobdella*; multiple origins of the terrestrial blood-sucking *Haemadipsa* Tennent, 1859 in Japan; and the low genetic divergence of freshwater predatory genus *Mimobdella* Blanchard, 1897b.

12.4 *Orobdella*, the Most Diverse Leech Genus in Japan

12.4.1 Species Diversity and Morphological Characteristics

Until recently, the genus *Orobdella* had contained only 4 species inhabiting Japan and Primorsky Krai, the Russian Far East (Sawyer 1986). Since 2010, however, several taxonomic and molecular phylogenetic studies have been conducted on *Orobdella*, and these studies have revealed high diversity of this genus (Nakano 2010, 2012b). According to the latest taxonomic study on this genus (Nakano 2014), 12 species have been recognized under *Orobdella*: 10 species are endemic to Japan, known from Hokkaido, Honshu, Kyushu, and the Ryukyu Islands; 1 species inhabits the Korean Peninsula and adjacent islets, including Tsushima Island; and 1 species is endemic to Taiwan (Table 12.2).

These 12 species can be divided into morphological groups by two characteristics: mid-body somite annulation and the body size of mature individuals (Table 12.2). Based on mid-body somite annulation, *Orobdella* species are grouped into three types: mid-body somites divided into four annuli (quadrannulate), six annuli (sexannulate), and eight annuli (octannulate). According to the body size of

Table 12.2 Twelve described *Orobdella* species with information on mid-body somite annulation type, body size type, and distributional range

	Morphological characters		
Species	Mid-body somite annulation	Body size	Distribution
Hokkaido lineage			
O. kawakatsuorum Richardson, 1975	Quadrannulate	Middle	Hokkaido and adjacent islets[d, h]
O. koikei Nakano, 2012b	Quadrannulate	Small	Hokkaido[d]
Honshu lineage			
O. ijimai Oka, 1895b	Sexannulate	Middle	Northern Kanto region in Honshu[c, d]
O. masaakikuroiwai Nakano, 2014	Quadrannulate	Small	Chubu and Kanto regions in Honshu[g]
O. octonaria Oka, 1895b	Octannulate	Large	Kanto to Chubu region in Honshu[d, e, l, m]
O. whitmani Oka, 1895b*	Quadrannulate	Middle	Chubu and Kinki regions in Honshu[a]
Korean Peninsula to Taiwan lineage			
O. dolichopharynx Nakano, 2011c	Sexannulate	Middle	Amamioshima Island, Ryukyu Islands[c]
O. esulcata Nakano, 2010	Quadrannulate	Middle	Northern Kyushu and Ikinoshima Island[a, d]
O. ketagalan Nakano and Lai, 2012	Quadrannulate	Middle	Taiwan[i]
O. mononoke Nakano, 2012a	Sexannulate	Middle	Yakushima Island, Ryukyu Islands[f]
O. shimadae Nakano, 2011c	Sexannulate	Middle	Okinawajima Island, Ryukyu Islands[c]
O. tsushimensis Nakano, 2011b	Quadrannulate	Middle	Korean Peninsula and adjacent islets including Tsushima Island[b, j, k]

Species marked with an asterisk (*) represents the type species of the genus

Sources: [a]Nakano (2010), [b]Nakano (2011b), [c]Nakano (2011c), [d]Nakano (2012b), [e]Nakano (2012c), [f]Nakano (2012a), [g]Nakano (2014), [h]Nakano and Gongalsky (2014), [i]Nakano and Lai (2012), [j]Nakano and Seo (2012), [k]Nakano and Seo (2014), [l](Oka (1895b), [m]Richardson (1975)

mature individuals, however, the 12 species are divided into three groups as follows: body size less than 4 cm (small type), body length to about 10 cm (middle type), and body length often greater than 15 cm (large type).

12.4.2 Phylogenetic Relationships of Known Species

Molecular phylogenetic analyses of the known *Orobdella* species (Nakano 2012a, 2014) showed that *Orobdella* divided into two main lineages, and the lineage consisting only of two species inhabiting Hokkaido and neighboring islets is a sister group to the lineage containing the remaining ten species, distributed in the south of Hokkaido (Fig. 12.2). Additionally, four species known in the Ryukyu Islands and Taiwan are grouped phylogenetically with two species distributed in the Korean Peninsula and adjacent islets as well as Kyushu.

The distribution of *Orobdella* is restricted to Primorsky Krai, the Korean Peninsula, the Japanese Archipelago, and Taiwan. *Orobdella* has not been recorded in continental China to date. Thus, it is possible that the last common ancestor of all species of *Orobdella* might be distributed in the northeastern margin of the Asian mainland, present-day Primorsky Krai, the Korean Peninsula, and the Japanese Archipelago. In addition to its geographic traits, molecular phylogenies of *Orobdella* indicated that the sexannulate mid-body somite annulation and small type of body length evolved in parallel within this genus (Fig. 12.2).

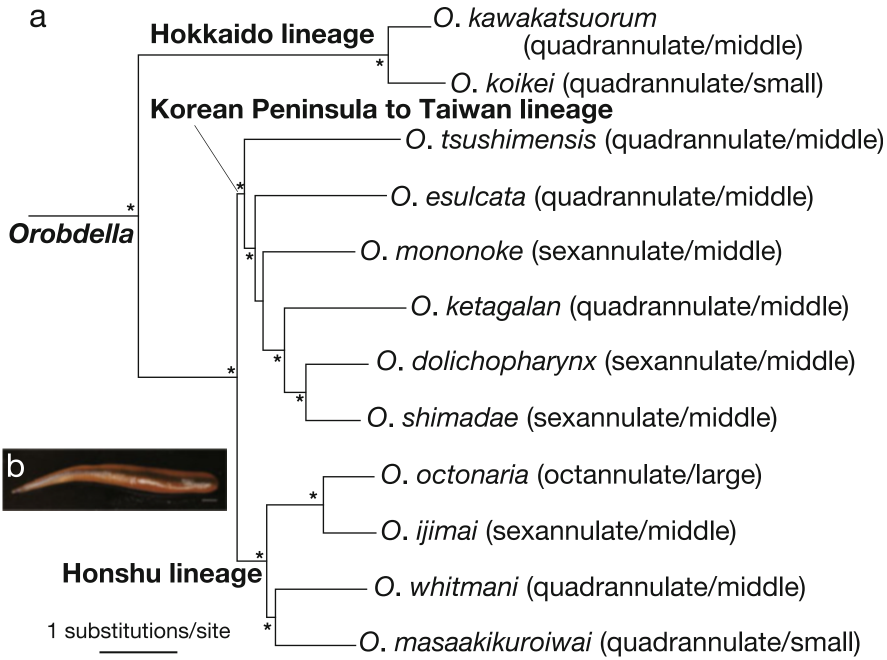

Fig. 12.2 Phylogenetic relationships of the known *Orobdella* species. (**a**) The maximum-likelihood tree of nuclear and mitochondrial markers with information on the mid-body somite annulation and body size. (Modified from Nakano, 2014) *Asterisks* (*) with nodes indicate bootstrap values for maximum-likelihood greater than 70 % and Bayesian posterior probabilities higher than 95 %. (**b**) *Orobdella whitmani* Oka, 1895b from Honshu. *Bar* 5 mm

Although the distributional range of *Orobdella* is quite restricted, the number of the known species is quite large. Because 11 species of this genus inhabit the Japanese Archipelago, including Tsushima Island and the Ryukyu Islands, this genus is the most diverse taxon among the leech genera known in Japan. It has often been suggested that hematophagous leeches were dispersed with their host animals, such as European *Hirudo* species in Trontelj and Utevsky (2012) and avian-parasite *Theromyzon tessulatum*, as reviewed in Sawyer (1986). However, *Orobdella* leeches are macrophagous species that feed on earthworms. Thus, the distribution of *Orobdella* species has been affected by their dispersal abilities. Additionally, *Orobdella* leeches are terrestrial species. Taking these ecological traits into account, *Orobdella* has possibly been more highly influenced by geological events and geographic boundaries than other hematophagous or aquatic leech taxa.

12.4.3 Distribution Pattern of Known Orobdella *Species in Japan*

Comparing the number of known *Orobdella* species in Taiwan as well as the Korean Peninsula, *Orobdella* species are most highly diversified in Japan (Fig. 12.3). First, both the main lineages of *Orobdella* occur in the Japanese Archipelago, and each lineage has diversified in Japan. Additionally, the 11 species in Japan can be grouped into two geographic patterns according to the distribution range of each Japanese species: allopatric and sympatric. Three species, *O. dolichopharynx* Nakano, 2011c, *O. mononoke* Nakano, 2012a and *O. shimadae* Nakano, 2011c, are known in the Ryukyu Islands, each of which is indigenous to a specific island. Thus, it seems possible that the diversification of *Orobdella* species known in the Ryukyu Islands occurred allopatrically through geological events in the region. In contrast, the small-type species and middle-type species are distributed sympatrically in Hokkaido (small *O. koikei* Nakano, 2012b and middle *O. kawakatsuorum* Richardson, 1975) as well as Honshu (small *O. masaakikuroiwai* Nakano, 2014 and middle *O. whitmani* Oka, 1895b). Based on this sympatric distribution pattern, Nakano (2014) suggested that a difference in body size of mature individuals within *Orobdella* species may enable different species to coexist in the same region. It is also significant that sexannulate and octannulate species have only been recorded in Japan.

To examine the history of diversification of *Orobdella* species in Japan, phylogeographic analyses should be conducted by integration with geological history in this region. Additionally, a character state reconstruction in *Orobdella* is necessary, focusing on mid-body somite annulation and body size. However, Nakano (2014) mentioned that several undescribed species had also been recognized in Japan. Nakano and Lai (2012) also stated that the *Orobdella* species diversity in Taiwan remained unclear. Above all, further faunal and taxonomic

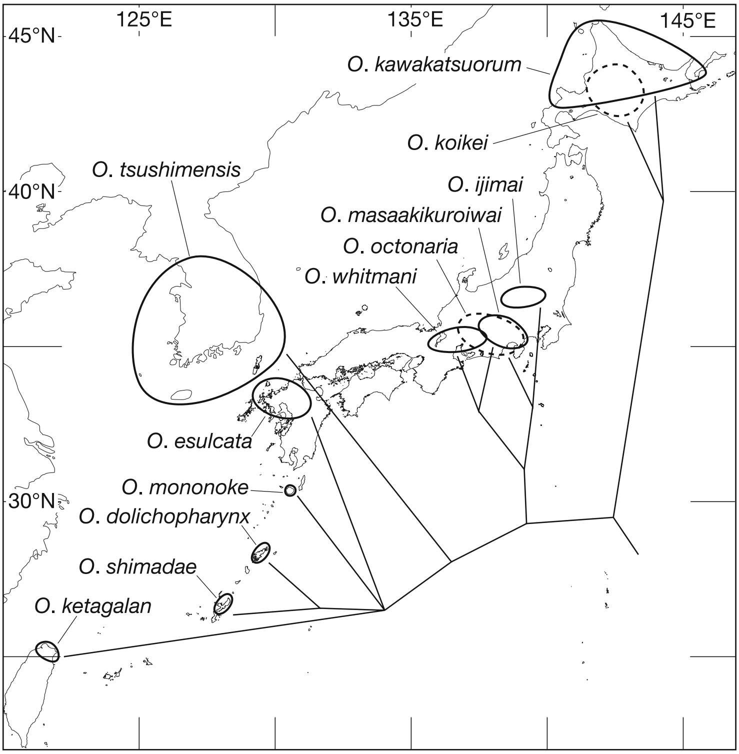

Fig. 12.3 Phylogeographic relationships among known species of *Orobdella*

studies should be conducted to reveal the true species diversity of this genus. The distribution of each known species should be also determined. Based on such fundamental taxonomic research, future studies will be able to reveal how *Orobdella* species have become highly diversified in Japan.

12.5 Multiple Origins of Haemadipsid Species in Japan

The genus *Haemadipsa* is a leech taxon well known as terrestrial blood-suckers. In Japan, three species group taxa of this genus have been recorded (Fig. 12.4): *H. japonica*, *H. zeylanica ivosimae* Oka, 1930, and *H. rjukjuana* Oka, 1910a.

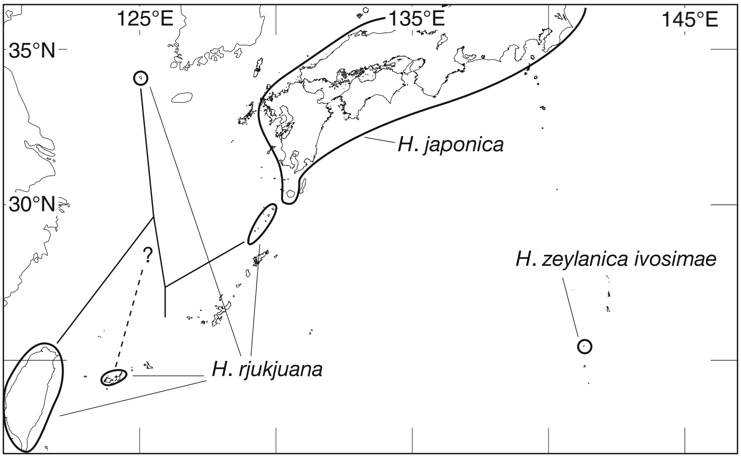

Fig. 12.4 Distributions of the species of *Haemadipsa* in Japan, and phylogeographic relationships of *H. rjukjuana*. (According to Won et al. 2014)

12.5.1 *Enigmatic* Haemadipsa *Species Recorded on a Volcanic Island*

Haemadipsa z. ivosimae has only been recorded on Kita-Ioto island in the Ogasawara Islands. However, the taxonomic status and phylogenetic position of *H. z. ivosimae* remain uncertain, because this species has not been revised since its original description. Thus, the taxonomic status of this taxon should be clarified based on its syntypes or newly collected materials. In addition, Oka (1930) noted that this species infected the eyes of birds at this location. Because Kita-Ioto island is a volcanic island and has never been connected to mainland masses, it is possible that this taxon invaded the island along with avian hosts. It has often been mentioned that haemadipsid species have been dispersed via their avian host species (see Borda and Siddall 2011). However, there has been no precise record of bird species with long-distance dispersal ability as hosts for haemadipsid species (Borda and Siddall 2011). Field surveys of its avian hosts should be conducted to examine the invasion event of this taxon to Kita-Ioto island.

12.5.2 *Different Origins of* Haemadipsa japonica *and* H. rjukjuana

The distributional boundary between the two *Haemadipsa* species, *H. japonica* and *H. rjukjuana*, is located in the northern part of the Ryukyu Islands between Yakushima island and the Tokara Islands. Although *Haemadipsa japonica* is distributed in Honshu, Shikoku, Kyushu, and Yakushima Island (Tani and Ishikawa

2005; Oka 1910b), *Haemadipsa rjukjuana* has been recorded from the Tokara Islands and Yaeyama Islands in the Ryukyu Islands, and Taiwan (Lai and Chen 2010; Lai et al. 2011). The former species has been also reported in continental China (Yang 1996). The latter was recently recorded from Gageodo Island, a small islet adjacent to the Korean Peninsula (Seo et al. 2013).

It has been recognized that these two species do not form a monophyly. A recent molecular phylogenetic study showed that *Haemadipsa rjukjuana* was a sister species to *Haemadipsa* species collected in Guangxi Zhuang Autonomous Region, in the southern part of China (Borda and Siddall 2011). Although they could not determine a precise phylogenetic position of *H. japonica* within the genus, the molecular phylogeny showed that *H. japonica* is close to the two species collected in Thailand and Nepal. Thus, it seems clear that the colonization history of *H. japonica* and that of *H. rjukjuana* are quite different.

12.5.3 Phylogenetic Relationships Within **Haemadipsa rjukjuana**

Although molecular data from *Haemadipsa rjukjuana* in Ishigakijima Island, located in the southern part of the Ryukyu Islands (the type locality of this species), were not included, molecular phylogenetic relationships of this species have been assessed based on specimens collected from Taiwan, the Tokara Islands, and Gageodo island (Won et al. 2014) (Fig. 12.4). Their molecular phylogenies showed that the individual from the Tokara Islands is a sister lineage to the clade consisting of the Taiwanese *H. rjukjuana* and the Gageodo individuals. Gageodo island is about 50 km from the Tokara Islands and about 1100 km from Taiwan. Moreover, the Tokara Islands are about 1000 km from Taiwan. The demonstrated phylogenetic relationships of *H. rjukjuana* revealed an incongruence between its genetic structure and geographic distances among these localities. The phylogenetic relationships and distributional patterns suggest that the present distribution of *H. rjukjuana* has possibly been accomplished via long-distance migrants, as for *H. zeylanica ivosimae*.

12.6 Low Genetic Diversity of the Predatory Genus *Mimobdella*

12.6.1 Taxonomic Accounts of **Mimobdella** *and the Allied Genus* **Odontobdella**

Mimobdella japonica is the salifid freshwater predatory species and the type species of the genus. When the genus *Odontobdella* Oka, 1923 was established, Oka (1923) described that *Odontobdella* possessed stylets, one of the diagnostic characteristics of the family Salifidae, in the anterior end of the pharynx, whereas *Mimobdella japonica* does not possess any structure in the pharynx. Nakano (2011a) examined the holotype of *M. japonica* and revealed that this species also possessed pharyngeal stylets and placed the genus *Mimobdella* under Salifidae.

A recent molecular phylogenetic study revealed that *Mimobdella* and *Odontobdella* formed a monophyletic lineage (Nakano et al. 2012). Nakano (2011a) stated that further taxonomic studies were necessary to determine the taxonomic status of *Odontobdella*, because the morphological characteristics of *O. blanchardi*, the type species of this genus, closely resemble those of *Mimobdella japonica*. However, the precise taxonomic account of *Odontobdella* has yet to be clarified.

12.6.2 Low Genetic Diversity of Mimobdella *in Japan*

Mimobdella japonica has been reported on Amamioshima and Okinawajima Islands in the Ryukyu Islands (Nakano 2013). Based on COI sequences obtained from specimens from Amamioshima and Okinawajima Islands, *M. japonica* distributed on these islands had identical COI sequences. In contrast, as already mentioned, molecular data from two *Orobdella* species distributed on these two islands showed that these two species are highly genetically diverged (Nakano 2014).

Nakano (2013) stated that the low genetic diversity of *M. japonica* might indicate that this species was introduced via human activities or dispersed to these islands in a recent rapid range expansion. He also mentioned that the confirmed distribution of *Mimobdella japonica* was restricted to these two islands. Oka (1910b) noted that *Odontobdella blanchardi* was collected on Okinawajima Island. As noted, the morphological characteristics of *O. blanchardi* closely resemble those of *M. japonica*. Thus, it seems possible that Oka (1910b), in fact, misidentified *M. japonica* on Okinawajima Island as *O. blanchardi*. If he actually misidentified *M. japonica* as *O. blanchardi*, *M. japonica* possibly invaded from Okinawajima Island to Amamioshima Island. Clearly, further taxonomic surveys are essential to finally clarify whether *M. japonica* is truly an alien species.

12.7 Conclusions

The Japanese Archipelago is mountainous and consists of a vast number of large islands as well as islets. The geography of the archipelago is considered to have had a large influence on the high species diversity of the terrestrial and macrophagous species of *Orobdella*. However, the obtained phylogenetic relationships of

Haemadipsa rjukjuana emphasize that relationships with host species should be taken into account when considering the evolutionary history of parasitic leech species. The low genetic diversity of *Mimobdella* and the presence of the freshwater invasive leech species have shed light on the possibility of the influence of human activities on the present distributions of freshwater leech species.

Not only molecular data, but also morphological and distributional information of many of the leech species known in Japan, should be revisited in future studies. Nakano (2010) mentioned that part of Oka's leech collection was deposited at the National Museum of Nature and Science, Tokyo (NSMT). Thus, based on the collection at NSMT, future taxonomic studies should be conducted to clarify the taxonomic status of the leech species described by Oka. After the taxonomic status of each of the known species is settled, the true species diversity and diversification history of leeches in Japan will become clear. Because recent taxonomic studies have revealed that the species number of *Orobdella* is higher than was previously thought, the species diversity of free-living leech species in Japan may be more diverse. When the biogeographic history of leeches in Japan is determined, faunistic exchanges and relationships between Japan and adjacent regions should be taken into account. Thus, Asian-wide systematic studies of leeches should also be conducted.

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Note Added in Proof After this manuscript was accepted for publication, 4 new species of *Orobdella* have been described from the western part of Honshu, and Shikoku, Japan (Nakano 2016a, b). *Orobdella brachyepididymis* Nakano, 2016b and *O. naraharaetmagarum* Nakano, 2016a are small type quadrannulate species belonging to the Korean Peninsula to Taiwan lineage, whereas the middle type sexannulate *O. okanoi* Nakano, 2016b and *O. yamaneae* Nakano, 2016b, and the large type octannulate *O. nakahamai* Nakano, 2016b are phylogenetically close to the Honshu lineage species (Nakano 2016b).

Mimobdella japonica has been also recorded from the volcanic Hachijojima Island, Izu Islands, Japan (Nakano and Meyer-Rochow 2016). Mitochondrial DNA sequences of the specimens from the island revealed that they had identical sequences to those obtained from *M. japonica* distributed in the Ryukyu Islands (Nakano and Meyer-Rochow 2016).

References

Apakupakul K, Siddall ME, Burreson EM (1999) Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. Mol Phylogenet Evol 12 (3):350–359. doi:10.1006/mpev.1999.0639

Bielecki A, Świątek P, Cichocka JM, Siddall ME, Urbisz AZ, Płachno BJ (2014) Diversity of features of the female reproductive system and other morphological characters in leeches (Citellata, Hirudinida) in phylogenetic conception. Cladistics 30(5):540–554. doi:10.1111/cla.12058

Blanchard R (1888) Hirudinées. In: Dechambre A, Lereboullet L (eds) Dictionnaire Encyclopédique des Sciences Médicales. Quatrième Série, vol 14. Masson, Asselin et Houzeau, Paris, pp 129–162

Blanchard R (1896) Description de quelques Hirudinées asiatiques. Mem Soc Zool Fr 9:316–330

Blanchard R (1897a) Hirudinées des Indes néerlandaises. In: Weber M (ed) Zoologische ergebnisse einer reise in Niederländisch Ost-Indien, vol 4. E. J. Brill, Leiden, pp 332–356

Blanchard R (1897b) Hirudinées du Musée de Leyde. Notes Leyd Mus 19(1-2):73–113

Borda E, Siddall ME (2004) Arhynchobdellida (Annelida: Oligochaeta: Hirudinida): phylogenetic relationships and evolution. Mol Phylogenet Evol 30(1):213–225. doi:10.1016/j.ympev.2003.09.002

Borda E, Siddall ME (2011) Insights into the evolutionary history of Indo-Pacific bloodfeeding terrestrial leeches (Hirudinida : Arhynchobdellida : Haemadipisidae). Invertebr Syst 24 (5):456–472. doi:10.1071/IS10013

Borda E, Oceguera-Figueroa A, Siddall ME (2008) On the classification, evolution and biogeography of terrestrial haemadipsoid leeches (Hirudinida: Arhynchobdellida: Hirudiniformes). Mol Phylogenet Evol 46:142–154. doi:10.1016/j.ympev.2007.09.006

Burreson EM, Kearn GC (2000) *Rhopalobdella japonica* n. gen., n. sp. (Hirudinea, Piscicolidae) from *Dasyatis akajei* (Chondrichthyes: Dasyatididae) in the northwestern Pacific. J Parasitol 86(4):696–699. doi:10.1645/0022-3395(2000)086[0696:RJNGNS]2.0.CO;2

Dutrochet H (1817) Note sur un Annélide d'un genre nouveau. Bull Sci Soc Philomat Paris 1817:130–131

Furiness S, Williams JI, Nagasawa K, Burreson EM (2007) A collection of fish leeches (Hirudinida: Piscicolidae) from Japan and surrounding waters, including redescriptions of three species. J Parasitol 93(4):875–883

Itoh T (2001) Morphological variation in Japanese populations of a freshwater leech, *Helobdella stagnalis* (Hirudinea: Rhynchobdellida: Glossiphoniidae). Species Divers 6(3):169–178

Itoh T (2010) Leeches as environmental indicators: based on fundamental knowledge of taxonomy and ecology of leeches. In: Tanida K (ed) Bioindicator of riverine environment. Hokuryukan, Tokyo, pp 103–112

Keegan HL, Toshioka S, Suzuki H (1968) Blood sucking Asian leeches of families Hirudidae and Haemadipsidae. Bio-Med Rep 406 Med Lab (16):i–iv + 1–130

Kovalenko MV, Utevsky SY (2015) Comparative structural analysis of jaws of selected blood-feeding and predacious arhynchobdellid leeches (Annelida: Clitellata: Hirudinida). Zoomorphology 134(1):33–43. doi:10.1007/s00435-014-0245-4

Lai Y-T, Chen J-H (2010) Leech fauna of Taiwan. National Taiwan University Press, Taipei

Lai Y-T, Chang C-H, Chen J-H (2009) Two new species of *Helobdella* Blanchard 1896 (Hirudinida: Rhynchobdellida: Glossiphoniidae) from Taiwan, with a checklist of Hirudinea fauna of the island. Zootaxa 2068:27–46

Lai Y-T, Nakano T, Chen J-H (2011) Three species of land leeches from Taiwan, *Haemadipsa rjukjuana* comb. n., a new record for *Haemadipsa picta* Moore, and an updated description of *Tritetrabdella taiwana* (Oka). ZooKeys 139:1–22. doi:10.3897/zookeys.139.1711

Linnaeus C (1758) Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Diferentiis, Stinontmis, Locis, 10th edn. Salvius, Stockholm

Moore JP (1918) The leeches (Hirudinea). In: Ward HB, Whipple GC (eds) Freshwater biology, 1st edn. Wiley, New York, pp 646–660

Müller OF (1774) Vermivm Terrestrium et Fluviatilium, seu Animalium Infusoriorum, Helminthicorum et Testaceorum, non Marinorum, Succincta Historia, vol 1, part 2. Heineck et Faber, Havniae et Lipsiae

Nagasawa K, Tanaka M (2012) *Limnotrachelobdella sinensis* (Hirudinida: Piscicolidae) parasitic on Japanese crucian carp (*Carassius cuvieri*) in game-fishing ponds in central Japan. Biogeography 14:99–104

Nagasawa K, Uyeno D (2009) *Zeylanicobdella arugamensis* (Hirudinida, Piscicolidae), a leech infesting brackish-water fishes, new to Japan. Biogeography 11:125–130

Nagasawa K, Yamauchi T, Umino T (2008) Synopsis of leeches of the families Piscicolidae and Ozobnrachidae (Annelida, Rhynchobdellida) in Japan. Bull Biogeogr Soc Jpn 63:151–171

Nagasawa K, Park S-W, Kim Y-G, Kim HJ (2009) *Limnotrachelobdella sinensis*, a leech associated with mortality in a wild population of Japanese crucian carp *Carassius cuvieri* in Korea. J Grad Sch Biosp Sci Hiroshima Univ 48:49–53

Nakano T (2010) A new species of the genus *Orobdella* (Hirudinida: Arhynchobdellida: Gastrostomobdellidae) from Kumamoto, Japan, and a redescription of *O. whitmani* with the designation of the lectotype. Zool Sci 27(11):880–887. doi:10.2108/zsj.27.880

Nakano T (2011a) Holotype redescription of *Mimobdella japonica* (Hirudinida, Arhynchobdellida, Erpobdelliformes) and taxonomic status of the genus *Mimobdella*. ZooKeys 119:1–10. doi:10.3897/zookeys.119.1501

Nakano T (2011b) A new species of *Orobdella* (Hirudinida: Arhynchobdellida: Gastrostomobdellidae) from Tsushima Island, Japan. Species Divers 16(1-2):39–47

Nakano T (2011c) Redescription of *Orobdella ijimai* (Hirudinida: Arhynchobdellida: Gastrostomobdellidae), and two new species of *Orobdella* from the Ryukyu Archipelago, Japan. Zootaxa 2998:1–15

Nakano T (2012a) A new sexannulate species of *Orobdella* (Hirudinida, Arhynchobdellida, Orobdellidae) from Yakushima Island, Japan. ZooKeys 181:79–93. doi:10.3897/zookeys.181.2932

Nakano T (2012b) A new species of *Orobdella* (Hirudinida, Arhynchobdellida, Gastrostomobdellidae) and redescription of *O. kawakatsuorum* from Hokkaido, Japan with the phylogenetic position of the new species. ZooKeys 169:9–30. doi:10.3897/zookeys.169.2425

Nakano T (2012c) Redescription of *Orobdella octonaria* (Hirudinida: Arhynchobdellida: Orobdellidae) with designation of a lectotype. Species Divers 17(2):227–233. doi:10.12782/sd.17.2.227

Nakano T (2013) First record of *Mimobdella japonica* (Hirudinida: Arhynchobdellida: Salifidae) from Okinawajima island, Ryukyu Islands, Japan, with a description of the specimens from the Ryukyu Islands. Species Divers 18(1):99–103. doi:10.12782/sd.18.1.099

Nakano T (2014) A new quadrannulate species of *Orobdella* (Hirudinida, Arhynchobdellida, Orobdellidae) from central Honshu, Japan. ZooKeys 445:57–76. doi:10.3897/zookeys.445.7999

Nakano T (2016a) A new quadrannulate species of Orobdella (Hirudinida, Arhynchobdellida, Orobdellidae) from western Honshu, Japan. ZooKeys 553:33–51. doi:10.3897/zookeys.553.6723

Nakano T (2016b) Four new species of the genus Orobdella from Shikoku and Awajishima island, Japan (Hirudinida, Arhynchobdellida, Orobdellidae). Zoosyst Evol 92(1):79–102. doi:10.3897/zse.91.7616

Nakano T, Gongalsky KB (2014) First record of *Orobdella kawakatsuorum* (Hirudinida: Arhynchobdellida: Erpobdelliformes) from Kunashir Island, Kuril Islands. Biodivers Data J 2:e1058. doi:10.3897/BDJ.2.e1058

Nakano T, Itoh T (2011) A list of the leech (Clitellata: Hirudinida) collection deposited in the Department of Zoology, The University Museum, The University of Tokyo. Univ Mus Univ Tokyo Mat Rep 90:85–94

Nakano T, Lai Y-T (2012) A new species of *Orobdella* (Hirudinida, Arhynchobdellida, Orobdellidae) from Taipei, Taiwan. ZooKeys 207:49–63. doi:10.3897/zookeys.207.3334

Nakano T, Meyer-Rochow VB (2016) First record of Mimobdella japonica (Hirudinida: Arhynchobdellida: Salifidae) from Hachijojima island, Izu Islands, Japan, with a comment on the genetic diversity of the species. Species Divers 21(1):49–54. doi:10.12782/sd.21.1.049

Nakano T, Seo H-Y (2012) First record of *Orobdella tsushimensis* (Hirudinida: Arhynchobdellida: Orobdellidae) from Korea (Gageodo Island) and its molecular phylogenetic position within the genus. Species Divers 17(2):235–240. doi:10.12782/sd.17.2.235

Nakano T, Seo H-Y (2014) First record of *Orobdella tsushimensis* (Hirudinida: Arhynchobdellida: Gastrostomobdellidae) from the Korean Peninsula and molecular phylogenetic relationships of the specimens. Anim Syst Evol Divers 30(2):87–94. doi:10.5635/ASED.2014.30.2.087

Nakano T, Sung Y-H (2014) A new host record for *Tritetrabdella taiwana* (Hirudinida: Arhynchobdellida: Haemadipsidae) from the Asian painted frog *Kaloula pulchra* (Anura: Microhylidae) in Hong Kong, China, with a taxonomic note on *T. taiwana*. Comp Parasitol 81(1):125–129. doi:10.1654/4667.1

Nakano T, Ramlah Z, Hikida T (2012) Phylogenetic position of gastrostomobdellid leeches (Hirudinida, Arhynchobdellida, Erpobdelliformes) and a new family for the genus *Orobdella*. Zool Scr 41(2):177–185. doi:10.1111/j.1463-6409.2011.00506.x

Nesemann H (1995) On the morphology and taxonomy of the Asian leeches (Hirudinea: Erpobdellidae, Salifidae). Acta Zool Acad Sci Hung 41(3):165–182

Nesemann H (1997) Rediscovery of the leech genus *Ancyrobdella* (Hirudinea, Glossiphoniidae). Misc Zool Hung 11:5–10

Oceguera-Figueroa A (2012) Molecular phylogeny of the New World bloodfeeding leeches of the genus *Haementeria* and reconsideration of the biannulate genus *Oligobdella*. Mol Phylogenet Evol 62(1):508–514

Oceguera-Figueroa A, Phillips AJ, Pacheco-Chaves B, Reeves WK, Siddall ME (2011) Phylogeny of macrophagous leeches (Hirudinea, Clitellata) based on molecular data and evaluation of the barcoding locus. Zool Scr 40(2):194–203. doi:10.1111/j.1463-6409.2010.00465.x

Ogawa K, Rusinek O, Tanaka M (2007) New record of the leech *Limnotrachelobdella sinensis* infecting freshwater fish from Japanese waters. Fish Pathol 42(2):85–89

Ohno M (2001) List of the Japanese wildlife. 45. Annelida, Hirudinea. In: Wildlife Division Nature Conservation Bureau of the Environmental Agency (ed) List of the Japanese wildlife: current status of the species of the Japanese wild animals and plants. Invertebrate III. Japan Wildlife Research Center, Tokyo, pp 47–49

Oka A (1895a) Description d'une espèce d'*Ozobranchus* (?*Oz. Mendiesi* Quatr.). Dobutsugaku Zasshi 7(75):1–7

Oka A (1895b) On some new Japanese land leeches. (*Orobdella* nov. gen.). J Coll Sci Imp Univ Jpn 8(2):275–306

Oka A (1910a) Key to Japanese leeches. Dobutsugaku Zasshi 22(256):56–64

Oka A (1910b) Synopsis der japanischen Hirudineen, mit Diagnosen der neuen Species. Annot Zool Jpn 7(3):165–183

Oka A (1912) Eine neue *Ozobranchus*-Art aus China. (*Oz. jantseanus* n. sp.). Annot Zool Jpn 8 (1):1–4

Oka A (1917) *Ancyrobdella biwae* n. g. n. sp., ein merkwürdiger Rüsselegel aus Biwa=See. Annot Zool Jpn 9(3):185–193

Oka A (1923) Sur les deux genres *Mimobdella* Blanchard et *Odontobdella* nov. gen. Annot Zool Jpn 10(6):243–252

Oka A (1925a) Notices sur les Hirudinées d'Extreme Orient, I–IV. Annot Zool Jpn 10(7):311–326

Oka A (1925b) Notices sur les Hirudinées d'Extrême Orient, V–VII. Annot Zool Jpn 10 (7):327–335

Oka A (1926) Notices sur les Hirudinées d'Extrême Orient, VIII. Annot Zool Jpn 11(1):59–62

Oka A (1927) Sur la morphologie externe de Pontobdelle. Proc Imp Acad 3(2):90–93. doi:10.2183/pjab1912.3.90

Oka A (1928) Description de l'*Hemiclepsis kasmiana*. Proc Imp Acad 4(2):64–66. doi:10.2183/pjab1912.4.64

Oka A (1929) Révision des Herpobdelles d'Extrême Orient. Proc Imp Acad 5(7):277–279. doi:10.2183/pjab1912.5.277

Oka A (1930) Sur une variété de l'*Haemadipsa zeylanica* s'attaquant aux Oiseaux. Proc Imp Acad 6(2):82–84. doi:10.2183/pjab1912.6.82

Oka A (1935) Apercu de la faune hirudinéenne japonaise. Proc Imp Acad 11(6):240–241. doi:10.2183/pjab1912.11.240

Pawłowski LK (1962) O występowaniu pijawki *Erpobdella octoculata* (L.) w Japonii. Zesz Nauk Uniw Łódz Nauk Matema Ser II 12:127–136

Phillips AJ, Siddall ME (2009) Poly-paraphyly of Hirudinidae: many lineages of medicinal leeches. BMC Evol Biol 9:246. doi:10.1186/1471-2148-9-246

Phillips AJ, Arauco-Brown R, Oceguera-Figueroa A, Gomez GP, Beltrán M, Lai Y-T, Siddall ME (2010) *Tyrannobdella rex* n. gen. n. sp. and the evolutionary origins of mucosal leech infestations. PLoS One 5(4):e10057. doi:10.1371/journal.pone.0010057

Richardson LR (1971) Gastrostomobdellidae f. nov. and a new genus for the gastroporous *Orobdella octonaria* Oka, 1895, of Japan (Hirudinoidea: Arhynchobdellae). Bull Natl Sci Mus 14(4):585–602

Richardson LR (1975) A new species of terricolous leeches in Japan (Gastrostomobdellidae, *Orobdella*). Bull Natl Sci Mus Ser A (Zool) 1(1):39–56

Rousset V, Pleijel F, Rouse GW, Erséus C, Siddall ME (2006) A molecular phylogeny of annelids. Cladistics 22:1–23. doi:10.1111/j.1096-0031.2006.00128.x

Sawyer RT (1986) Leech biology and behaviour. Clarendon Press, Oxford

Seo H-Y, Eun Y, Park T-S, Kim K-G, Won S-H, Kim B-J, Kim H-W, Chae J-S, Nakano T (2013) First report of blood-feeding terrestrial leech, *Haemadipsa rjukjuana* Oka, 1910 (Hirudinida: Arhynchobdellida: Haemadipsidae) in Korea. Korean J Soil Zool 17(1-2):14–18

Siddall ME (2002) Phylogeny of the leech family Erpobdellidae (Hirudinida: Oligochaeta). Invertebr Syst 16(1):1–6. doi:10.1071/IT01011

Siddall ME, Burreson EM (1995) Phylogeny of Euhirudinea: independent evolution of blood feeding by leeches. Can J Zool 73(6):1048–1064

Siddall ME, Burreson EM (1998) Phylogeny of leeches (Hirudinea) based on mitochondrial cytochrome *c* oxidase subunit. Mol Phylogenet Evol 9(1):156–162

Siddall ME, Apakupakul K, Burreson EM, Coates KA, Erséus C, Gelder SR, Källersjö M, Trapido-Rosenthal H (2001) Validating Livanow: molecular data agree that leeches, branchiobdellidans, and *Acanthobdella peledina* form a monophyletic group of oligochaetes. Mol Phylogenet Evol 21(3):346–351. doi:10.1006/mpev.2001.1021

Siddall ME, Budinoff RB, Borda E (2005) Phylogenetic evaluation of systematics and biogeography of the leech family Glossiphoniidae. Invertebr Syst 19:105–112

Sket B, Trontelj P (2008) Global diversity of leeches (Hirudinea) in freshwater. Hydrobiologia 595:129–137. doi:10.1007/s10750-007-9010-8

Suzuki D, Ota H, Oh H-S, Hikida T (2011) Origin of Japanese populations of Reeves' pond turtle, *Mauremys reevesii* (Reptilia: Geoemydidae), as inferred by a molecular approach. Chelonian Conserv Biol 10(2):237–249. doi:10.2744/ccb-0885.1

Tani S, Ishikawa E (2005) Biology and control of land leech, *Haemadipsa zeylanica japonica*. For Pest 54(5):87–95

Tennent JE (1859) Ceylon: an account of the island, physical, historical, and topographical with notices of its natural history, antiquities and productions, vol 1, 1st edn. Longman, Green, Longman and Roberts, London

Trontelj P, Utevsky SY (2012) Phylogeny and phylogeography of medicinal leeches (genus *Hirudo*): fast dispersal and shallow genetic structure. Mol Phylogenet Evol 63(2):475–485. doi:10.1016/j.ympev.2012.01.022

Utevsky SY, Chernyshev AV (2013) A new genus and species of fish leeches *Dolichobdella rubra*, gen. n., sp. n. (Clitellata, Hirudinida, Piscicolidae), from the northern Sea of Japan. Deep-Sea Res Part II Top Stud Oceanogr 86-87:221–224. doi:10.1016/j.dsr2.2012.08.016

Utevsky SY, Trontelj P (2004) Phylogenetic relationships of fish leeches (Hirudinea, Piscicolidae) based on mitochondrial DNA sequences and morphological data. Zool Scr 33(4):375–385. doi:10.1111/j.0300-3256.2004.00156.x

Utevsky SY, Utevsky AY, Schiaparelli S, Trontelj P (2007) Molecular phylogeny of pontobdelline leeches and their place in the descent of fish leeches (Hirudinea, Piscicolidae). Zool Scr 36 (3):271–280

Whitman CO (1884) The external morphology of the leech. Proc Am Acad Arts Sci 20:76–87

Whitman CO (1886) The leeches of Japan. Q J Microsc Sci N S 26(103):317–416

Won S, Park B-K, Kim B-J, Kim H-W, Kang J-G, Park T-S, Seo H-Y, Eun Y, Kim K-G, Chae J-S (2014) Molecular identification of *Haemadipsa rjukjuana* (Hirudiniformes: Haemadipsidae) in Gageo Island, Korea. Korean J Parasitol 52(2):169–175. doi:10.3347/kjp.2014.52.2.169

Yamauchi T, Suzuki D (2008) Geographical distribution of *Ozobranchus jantseanus* (Annelida: Hirudinida: Ozobranchidae). Med Entomol Zool 59(4):345–349

Yamauchi T, Nishibori T, Suzuki D (2012) First report of *Ozobranchus jantseanus* (Hirudinida: Ozobranchidae) parasitizing the exotic red-eared slider *Trachemys scripta elegans* in Japan. Comp Parasitol 79(2):348–349. doi:10.1654/4553.1

Yamauchi T, Yoshigou H, Itoh T (2013) Occurrence of *Parabdella quadrioculata* (Annelida: Hirudinida: Glossiphoniidae) in Japan, with a first case of human infestation by the leech. Comp Parasitol 80(1):134–135. doi:10.1654/4593.1

Yang T (1996) Annelida Hirudinea. Fauna Sinica. Science Press, Beijing

Part III
Marine Invertebrates

Chapter 13
Taxonomic Review of Japanese Sponges (Porifera)

Yuji Ise

Abstract The history of taxonomic studies on Japanese sponges is reviewed. A literature-based list of Japanese sponge species is provided (see Appendix), which includes 636 species plus 16 subspecies, represented by all four classes in the phylum Porifera. Demosponges (Demospongiae) are the most predominant and consist of 434 species, followed by calcareous sponges (Calcarea, 119 spp.), hexactinellid or glass sponges (Hexactinellida, 78 spp.), and homoscleromorph sponges (Homoscleromorpha, 5 spp.). Most of the species are poorly understood, and the taxonomic identity of each species should be investigated in future studies. *Haliclona hoshinoi* nom. nov. is herein proposed for *Haliclona punctata* Hoshino, 1981 (type locality: Ariake Sea, Japan) to avoid homonymy with *Haliclona punctata* Bergquist and Warne, 1980 (type locality: Christchurch, New Zealand).

Keywords Systematics • Pacific Rim • Taxonomy • New replacement name • Taxonomic checklist

13.1 Introduction

Taxonomic research on Japanese sponges has been conducted by several scientists who focused individually on separate classes, or on marine or freshwater taxa. From the late nineteenth to early twentieth centuries, Isao Ijima (1861–1921) led research on the taxonomy of the class Hexactinellida Schmidt, 1870, and Sanji Hôzawa (1885–1947) worked on the taxonomy of the class Calcarea Bowerbank, 1862. From the mid-twentieth century, Senji Tanita (1908–1995) carried out taxonomic research on Calcarea and marine demosponges simultaneously. From the late twentieth century, Takaharu Hoshino (1947–1988) led taxonomic work on Japanese marine demosponges. Since the last works of Tanita and Hoshino until now, no comprehensive study of sponge taxonomy in Japan has been conducted except for that of freshwater sponges. A brief history of sponge science and a bibliography of

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Japanese sponge scientists was provided by Mizoguchi (1998). Thus, my primary purpose here is to focus on inventory of the marine sponge species that occur in Japanese waters, with respect to their taxonomy and the history of research. Masuda (2006) listed a total of 25 species in 11 genera of Japanese freshwater sponges (Class Demospongiae Sollas, 1885, Order Spongillida Manconi and Pronzato, 2002), and Kyodo (1934) and Masuda (2006) presented a brief history of taxonomic studies on the group.

I provide a list of all sponge species in Japanese waters (see Appendix), adopting the latest taxonomic scheme of the *World Porifera Database* (Van Soest et al. 2015a). However, this list should be regarded as a stepping-stone for future studies because I have accepted information in previous reports at face value, without making corrections based on actual observations of specimens. I hope that precise revisionary work based on type material and additional specimens will be carried out for the future of sponge science in Japan.

13.2 Brief History of Taxonomic Study of Japanese Sponges with Some Notes and Scope for Future Studies

13.2.1 Class Homoscleromorpha Bergquist, 1978

No comprehensive revisions on homoscleromorph sponges around Japan have been carried out, and only five species have been recorded previously (Ise 2013) (Appendix). Of these, the identity of *Plakortis simplex* Schulze, 1880 recorded by Hoshino (1987a) and that of *Plakina monolopha* Schulze, 1880 recorded by Tanita and Hoshino (1989) are dubious because the type localities of these two species are in the Mediterranean. Considering the short planktonic larval duration in these sponges, they were either simply misidentified (Lévi 1953; Muricy and Diaz 2002; Muricy 2011) or artificially introduced as ship-fouling fauna or via ship's ballast water. Future molecular work is required to confirm the taxonomic identities of these two species in Japanese waters. A preliminary research by our group, from the intertidal zone to a depth of about 300 m around Japan, has revealed the existence of species other than the five known species (Ise et al., unpublished data): these include species of the genus *Corticium*, a new genus record from Japan (Fig. 13.1a), and blue-colored *Plakina*. Inclusion of these species will result in more than 15 species in total around Japan (Ise, unpublished data, partly based on registered specimens in the National Museum of Nature and Science, Tokyo). An undescribed species of *Oscarella* has been found in several regions of Japan (Izumi et al., unpublished data). The genus *Oscarella* is globally well known because its member *Oscarella lobularis* (Schmidt, 1862) has been suggested as a model organism for evolutionary and developmental biology (Ereskovsky et al. 2009).

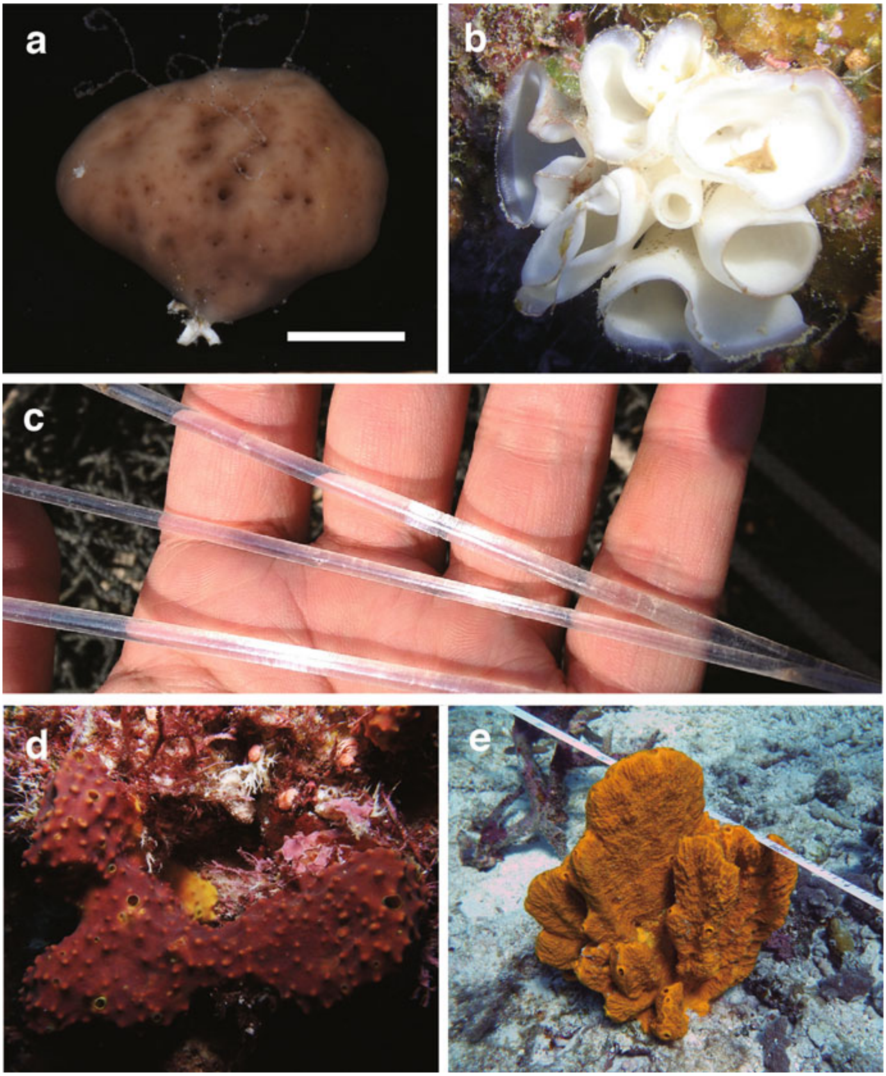

Fig. 13.1 (**a**) Homoscleromorph sponge *Corticium* sp. (Plakinidae, Homosclerophorida) collected from Shimoji Island, Miyako Islands, southern Japan, 21 m deep. *Scale* 4 mm. (**b**) Calcareous sponge *Paragrantia waguensis* (Grantiidae, Leucosolenida) from Shimoji Island, 28.2 m deep. (Photograph by M. Mizuyama.) (**c**) Giant glass rods of hexactinellid sponge *Monorhaphis chuni* (Monorhaphididae, Amphidiscosida) collected from off Okinoerabu Island, southern Japan, 1083–1093 m deep by beam trawl of R/V *Tansei-maru*. (**d**) *Suberea* sp. (Aplysinellidae, Verongiida, Demospongiae) from Shimoji Island, 25 m deep. (**e**) *Stylissa massa* (Scopalinidae, Scopalinida, Demospongiae) from Sawada beach, Shimoji Island, 2 m deep

13.2.2 Class Calcarea Bowerbank, 1862

The first scientific report that contributed to our knowledge of Japanese sponges was about the sponges in class Calcarea by Haeckel (1872), who described three new species and recorded one known species. Subsequently, Döderlein (1892) described a peculiar new species from Sagami Bay. Hara (1894) was the first Japanese who described a new species of calcareous sponge; Nakagawa (1897) reported an unidentified species of *Sycandra* from Kyushu. In the early twentieth century, Hôzawa (1916) commenced his taxonomic study of calcareous sponges, undertaking study of the *Albatross* collection of calcareous sponges supplied by Isao Ijima (see the following Sect. 13.2.3 Hexactinellida); Hôzawa (1918) described 13 species, of which 11 were new to science. After that, he conducted a series of studies (Hôzawa 1923, 1929, 1933a, b, c, 1940a, b, c; Row and Hôzawa 1931; Hôzawa and Tanita 1941, 1965) and listed 66 species as Japanese calcareous sponges (Hôzawa 1940c). Subsequently, Tanita (1939, 1940, 1941a, b, 1942a, b, c, 1948, 1958, 1965a) conducted works mainly on species in the northern part of Japan. Tanita (1943) listed 131 species as Japanese calcareous sponges, although 5 of these were from Palau. Ogawa (1999) rearranged Tanita's (1943) list according to the taxonomic scheme proposed by Burton (1963) and reduced the total number of species to 21 in 10 genera. However, this revision was very different from the current system and thus Hoshino et al. (2003) and Ise (in Fujikura et al. 2010) returned to Tanita's (1943) list and revised it under the scheme of *Systema Porifera* (Hooper and Van Soest 2002), concluding that there were 130 species in total.

In this work I have reviewed the previous lists of the Japanese calcareous sponge species in the light of the *World Porifera Database* (Van Soest et al. 2015a). I have omitted 2 species from Simushir Island, *Leucandra kurilensis* Hôzawa, 1918 and *Achramorpha diomediae* Hôzawa 1918; 1 species from Kuril Islands, *Leucopsila stylifera* (Schmidt, 1870); 1 species from Sakhalin, *Heteropia medioarticulata* Hôzawa, 1918; and 1 unknown name "*Leucandra consolida*," in Ogawa (1999). As the result, I listed 119 species (4 orders, 14 families, 28 genera) as Japanese calcareous sponges (Appendix). According to this list, 4 of the 5 known orders are recorded from Japan. Of these, Leucosolenida Hartman, 1958 (91 spp.) occupies about 76 % of the total species. *Petrostroma schulzei* Döderlein, 1892, the only species representing the order Lithonida Vacelet, 1981 recorded in Japan, is only known by the original description, with its identity remaining obscure. Among the Japanese calcareous sponges, this is the only species that possesses a hypercalcified skeleton and is considered as a possible extant 'pharetronid' (Vacelet et al. 2002); a rediscovery of this taxon is expected in future studies. *Leucyssa spongilla* Haeckel, 1872, 1 of the 2 species of the order Baerida Borojevic et al., 2000, has also not been rediscovered since its original description. No member of the order Murryonida Vacelet, 1981 has been recorded from Japanese waters yet; however, some may be found in future surveys, with potential habitats including submarine caves in the Ryukyu Islands, southern Japan.

As for families, 14 of the 23 known taxa are recorded from Japan. The major families are Grantiidae Dendy, 1893 (41 spp.) followed by Sycettidae Dendy, 1893 (23 spp.), Heteropiidae Dendy, 1893 (15 spp.), and Clathrinidae Minchin, 1900 (11 spp.). In Calcarea, four families consist of only 1 species. Of these, *Leucyssa spongilla* (Trichogypsiidae Borojevic et al., 2000) and *Petrostroma schulzei* (Minchinellidae Dendy and Row, 1913) have not been rediscovered since their original description, as mentioned earlier. *Paralelapia nipponica* (Hara, 1894), the sole species of the family Lelapiidae Dendy and Row, 1913, is also known only by the original description. No systematic study of Japanese calcareous sponges has been conducted since Tanita (1965a, c), with the taxonomic identity of the vast majority of 'known' species being left uncertain (but see Van Soest et al. 2015b).

A recent survey on coral reefs and in submarine caves in the Ryukyu Islands, southern Japan, and a deep-sea survey around Japan, have revealed many unknown calcareous sponges waiting formal description (Ise, unpublished data). Based on morphological and molecular data from specimens collected in Okinawa, Van Soest et al. (2015b) reported *Paragrantia waguensis* Hôzawa, 1940, confirming the validity of the monotypic genus *Paragrantia* Hôzawa, 1940, which had been synonymized with *Grantia* Fleming, 1828 (see also Fig. 13.1b).

13.2.3 Class Hexactinellida Schmidt, 1870

The first scientific report on Japanese hexactinellid sponges was conducted by Carter (1885), who described four species including one new species based on specimens collected from Sagami Bay. Subsequently, Schulze (1886, 1887) described the Japanese hexactinellids from the H.M.S. *Challenger* expedition. Gravier (1899), and Topsent (1928a, b) also contributed to early works on hexactinellid sponges in Japan.

From the 1890s to the early twentieth century, important samples were collected successively in Sagami Bay by technical staff at Misaki Marine Biological Station (MMBS) of the University of Tokyo, notably Kumakichi Aoki (1864–1940). By using these specimens, Ijima (1894, 1895, 1896, 1897, 1898, 1901, 1902a, b, c, 1903, 1904, 1916) successfully completed the most prominent and important work on hexactinellid sponges. After many years of struggle, a monograph of the *Siboga* Expedition report (Ijima 1927) was published (see Okada 1937; Reiswig 1990). Okada (1925) described a new genus and species of Hexactinellida (see also Ijima and Okada 1938). He also conducted the first developmental study of hexactinellid sponges in the world (Okada 1928) and was later in charge of the *Albatross* report (Okada 1932).

Since Okada (1925), there has been no comprehensive revision and description of Japanese hexactinellid sponges except a list of hexactinellid sponge specimens deposited in the University Museum, the University of Tokyo that was made by Ogawa et al. (2012). Ogawa (1997) compiled previous reports and listed 84 species in total as Japanese hexactinellid sponges. Hoshino et al. (2003) and Ise (in Fujikura et al. 2010) made minor revisions of Ogawa's (1997) list and concluded that there are 78 species in total.

In this chapter, I have reexamined the species lists by Ogawa (1997), Hoshino et al. (2003), and Ise (in Fujikura et al. 2010) under the latest scheme of the *World Porifera Database* (Van Soest et al. 2015a) and concluded that there are 78 species with 12 subspecies and 1 variety (in 34 genera, 9 families, 3 orders, and 2 subclasses) in Japanese waters (Appendix). Of these, 3 of the 5 known orders are recorded from Japan, of which Lyssacinosida Zittel, 1887 (43 spp., 4 subspp., and 1 var.) is the major taxon, followed by Hexactinosida Schrammen, 1912 (19 spp., 7 subspp.) and Amphidiscosida Schrammen, 1924 (16 spp., 1 subsp.). No representatives in the orders Aulocalycoida Tabachnick and Reiswig, 2000 and Lychniscosida Schrammen, 1903 have been recorded yet. As for the families, 9 of the 17 known taxa are recorded from Japan. Of these, Rossellidae Schulze, 1885 is predominant (29 spp., 3 subspp.), followed by Euretidae Zittel, 1877 (11 spp.), Euplectellidae Gray, 1867 (10 spp., 1 subsp.), and Hyalonematidae Gray, 1857 (9 spp.), almost all of which have been recorded from Sagami Bay.

In recent surveys employing deep-sea trawling around the Ryukyu Islands, giant glass rods of *Monorhaphis chuni* Schulze, 1904 (Amphidiscosida, Monorhaphididae Ijima, 1927) (Fig. 13.1c) have been frequently collected (Ise, unpublished data); this species will be added to the list of the Japanese sponge fauna in future studies with a formal description. In deep-sea trawling and dredging in the southern part of Japan, many other hexactinellid sponges have also been collected and are awaiting formal descriptions.

13.2.4 Class Demospongiae Sollas, 1885

The first record of Japanese marine demosponges was made by Döderlein (1883), who described three species of *Discodermia* Du Bocage, 1869 and one species of *Microscleroderma* Kirkpatrick, 1903 (as *Seliscothon* Zittel, 1878) from the deep-sea zone of Sagami Bay. Subsequent works comprised a part of a monograph of the H.M.S. *Challenger* Expedition (Poléjaeff 1884; Ridley and Dendy 1887; Sollas 1888). Carter (1885), Lampe (1886), and Lindgren (1897, 1898) also conducted works on demosponge fauna in Japan. Soon after the these works, Thiele (1898) made substantial contributions based on specimens collected by Döderlein and Franz M. Hilgendorf around Japan and described 87 species. Thiele (1898) also provided a brief history of studies on Japanese sponges at that time.

In the early 1900s, demosponge specimens, mainly in by-catch of hexactinellid sponges (see 13.2.3 Class Hexactinellida), were sent to Europe by Isao Ijima. By using these specimens, Lebwohl (1914a, b) focused on the order Tetractinellida Marshall, 1876 and described 36 species with 3 varieties. Topsent (1928b, 1930) described 6 species based on samples sent by Naohide Yatsu that included one possible carnivorous sponge, *Chondrocladia yatsui* Topsent, 1930. The first Japanese scientist who described marine demosponges was Kadota (1922), who described two common species from the intertidal rocky shore of the Miura Peninsula, *Halichondria japonica* (Kadota, 1922) and *Halichondria okadai* (Kadota, 1922) (both originally in *Reniera*).

Tanita (1958, 1961a, b, c, 1963, 1964, 1965a, b, c, 1967, 1968, 1969, 1970a, b, 1977, 1978) engaged in taxonomic studies of marine demosponges mainly in northern Japan, whereas Hoshino's (1970, 1971, 1974, 1975a, b, c, 1976a, b, c, Hoshino 1976d, 1977, 1981a, b, c, 1982, 1985a, b, c, 1986, 1987a, b, 1990) main field was the western part of Japan. During the late 1950s to late 1980s, Tanita and Hoshino led the taxonomy of Japanese sponges, culminating in a monograph of demosponges in Sagami Bay based on extensive material collected by Emperor Showa (Tanita and Hoshino 1989), wherein 161 species were described.

Hoshino (1986, 1987b) compiled a list of all the marine demosponges hitherto known in Japanese and adjacent waters, providing bibliographic citations for each original description, with 486 named species (including 17 subspp., 12 var., and 3 forms) and 2 unnamed species (Hoshino 1987b). In this list, Hoshino included species from Sakhalin, the Sea of Okhotsk, and the Kuril Islands described by Burton (1935) and Koltun (1958, 1959, 1962, 1966) and species from Korea (Rho and Sim 1976, 1979a, b, c, 1981a, b; Sim 1981a, b), Amoi (Lindgren 1897, 1898), and Shanghai (Sollas 1888). Ogawa (2001, 2002, 2003) revised Hosino's (1986) list by omitting 56 species recorded from the Kuril Islands and 88 species of unknown reference (but those references were included in Hoshino 1987b); by adding species of Sagami Bay (Tanita and Hoshino 1989), he concluded that there are 442 named species and 14 unnamed species in total in Japanese waters.

Since Tanita and Hoshino's (1989) Sagami Bay monograph, several contributions have been made to the Japanese marine demosponge fauna by Ogawa et al. (1993), Bavestrello et al. (1998), Calcinai et al. (2004, 2008), Ise et al. (2004), Ise and Fujita (2005), Hoshino et al. (2004, 2008), Ogawa (2006, 2010), Ogawa and Ito (2008), Higa et al. (2010), Ise and Vacelet (2010), Van Soest et al. (2010), Bertolino et al. (2011), and Otani (2012). By adding some of these newly recorded or described species, Hoshino et al. (2003) and Ise (in Fujikura et al. 2010) updated the total number of species in Japanese waters.

I examined Hoshino's (1987b) list and found that there are records of 20 species by Burton (1935) and 121 species (including 1 hydrozoan, 16 subspp., and 1 form) by Koltun (1958, 1959, 1962, 1966) from Sakhalin, the Sea of Okhotsk, and the Kuril Islands, 14 species from Korean waters (Rho and Sim 1976, 1979a, b, c, 1981a, b; Sim 1981a, b), 2 species from Amoi (Lindgren 1897, 1898), and 1 species from Shanghai (Sollas 1888). After omitting those species records from outside the Japanese exclusive economic zone, and by adding the latest records of Japanese sponges already mentioned, I revised the records in Ogawa (2001, 2002, 2003, 2004), Hoshino et al. (2003), and Ise (in Fujikura et al. 2010), adopting the taxonomic scheme of the latest version of *World Porifera Database* (Van Soest et al. 2015a) with the installment of a newly proposed system of class Demospongiae by Cárdenas et al. (2012) and Morrow and Cárdenas (2015).

Japanese marine demosponges include 408 named species plus 4 subspecies, 6 varieties, and 14 unnamed species in 118 genera, 57 families, 18 orders, and

3 subclasses (Appendix). By adding freshwater sponges (order Spongillida, family Spongillidae Gray, 1867), the total number reaches 434 named species (130 genera, 58 families, 19 orders). Of the 3 subclasses, Heteroscleromorpha Cárdenas et al. 2012 contains the overwhelming majority of speicies (410 spp. in 51 families), followed by Keratosa Grant, 1861 with 21 species (5 families) and Verongimorpha Erpenbeck et al., 2012 with 3 species (2 families). Twenty of the 22 known orders of demosponges in the world have been recorded from Japan, which means that the Japanese demosponge fauna almost entirely represents global diversity at the order level. The number of species is predominant in the orders Tetractinellida (99 spp.), Haplosclerida Topsent, 1928 (86 spp.), and Poecilosclerida Topsent, 1928 (71 spp.), whereas those in Polymastiida Morrow and Cárdenas, 2015 (4 spp.), Chondrillida Redmond et al., 2013 (2 spp.), Biemnida Morrow, 2013 (2 spp.), Desmacellida Morrow and Cárdenas, 2015 (2 spp.), Chondrosiida Boury-Esnault and Lopes, 1985 (1 sp.), Dendroceratida Minchin, 1900 (1 sp.), and Scopalinida Morrow and Cárdenas, 2015 (1 sp.) are few and likely to be underestimated. The two orders, Verongiida Bergquist, 1978 and Scopalinida, have not been formally recorded from Japanese waters by taxonomic papers. However, *Suberea* sp. (Aplysinellidae Bergquist, 1980) of the order Verongiida is common in some parts of southern Japan (Fig. 13.1d) and has been used for studies on secondary metabolites (Hirano et al. 2000; Tsuda et al. 2001); this unidentified species is not included in a list of Japanese sponges (Appendix). *Stylissa massa* (Carter, 1887) (Scopalinidae Morrow et al., 2012) of the order Scopalinida has also frequently been used for studies on bioactive compounds (Kita et al. 2003; Yamaguchi et al. 2003) and is very common in the shallow water of the Ryukyu Islands (Fig. 13.1e). The remaining two orders Sphaerocladina Schrammen, 1924 and Trachycladida Morrow and Cárdenas 2015 have not been discovered yet in Japan. *Vetulina stalactites* Schmidt, 1879 (Vetulinidae Lendenfeld, 1903), the sole species of the order Sphaerocladina, has only been known from the Caribbean (Pisera and Lévi 2002), and its distribution in Japan is thus unlikely. The reason for the absence of the order Trachycladida in Japanese waters is unknown; however, it might be discovered from the deep sea around Japan. Of the 92 known families of demosponges, 58 are recorded from Japan. Numbers of species are relatively well balanced among families compared to those of the orders. The major families are Chalinidae Gray, 1867 (42 spp.), Ancorinidae Schmidt, 1870 (27 spp.), Suberitidae Schmidt, 1870 (26 spp.), Spongillidae (26 spp.), and Callyspongiidae De Laubenfels, 1936 (24 spp.), followed by Halichondriidae Gray, 1867 (20 spp.), and then the number of species decreased to 1 species in each of 13 families. Of the unrecorded families, species of Rhabderemiidae Topsent, 1928 (Biemnida), Macandrewiidae Schrammen, 1924, Neopeltidae Sollas, 1888, Pleromidae Sollas, 1888, Azoricidae Sollas, 1888 (Tetractindellida), Crambeidae Lévi, 1963, Podospongiidae De Laubenfels, 1936 (Poecilosclerida), Hamacanthidae Gray, 1872 (Merliida Vacelet, 1979), and Timeidae Topsent, 1928 (Tethyida Morrow and Cárdenas, 2015) in Japanese waters are awaiting formal descriptions (Ogawa 2006 in part; Ise, unpublished data).

One striking result of a recent deep-sea survey in southern Japan is the discovery of a ‘living fossil,’ a colonial type of sphinctozoan sponge *Vaceletia* Pickett, 1974 of the family Verticillitidae Steinmann, 1882 that has been previously assigned to the order Verticillitida Termier and Termier in Termier et al., 1977 (now in the order Dictyoceratida Minchin, 1900) (Vacelet 2002; Wörheide 2008), which will be added to the Japanese sponge fauna (Ise, unpublished data).

From several rocky shores in temperate Japanese waters, certain demosponges have been reported under the names '*Callyspongia confoederata*' (Tanita 1961c, 1967, 1969, 1970b, 1977; Hoshino 1970, 1971, 1975a, c, 1976a, c, 1981a) and '*Callyspongia elegans*' (Tanita 1965a, 1970b, 1977; Tanita and Hoshino 1989). In these works, Tanita and Hoshino ascribed the identity of these taxa to Ridley (1884) and Thiele (1899), respectively. Although these Japanese '*Callyspongia confoederata*' and '*Callyspongia elegans*' are likely conspecific with each other (Ise, unpublished data), these are probably different from *C. confoederata* sensu Ridley (1884) from Torres Straits and *C. elegans* sensu Thiele (1899) from Sulawesi. Although the latter is a junior homonym of *Callyspongia elegans* (Lendenfeld, 1887), no new replacement name should be proposed before the taxonomic identity of these taxa is clarified. Also, the species status of the Japanese '*Callyspongia confoederata*' and '*Callyspongia elegans*' should be investigated in future studies.

The taxonomic identities of the two species *Halicona permollis* (Bowerbank, 1886) and *Halichondria japonica* Kadota, 1922, that both commonly occur in the intertidal to subtidal zones on temperate rocky shores in Japan, should be clarified by future molecular studies. The former is treated as a synonym of *Haliclona* (*Reniera*) *cinerea* (Grant, 1826) in Van Soest et al. (2015a), and the latter has been suggested as a species of *Hymeniacidon* by Hoshino et al. (2004, 2008).

'*Pachastrella loricata*' (Lebwohl, 1914), originally described as *Dercitus loricatus* from 'Doketsuba' in Sagami Bay (Lebwohl 1914a), is now treated as a *taxon inquirendum* (Van Soest et al. 2015a). The original description was likely based on a mixture of spicules from different species including *Pachastrella* cf. *monilifera* Schmidt, 1868 (Maldonado 2002), and '*Pachastrella tenuilaminaris*' [=?*Poecillastra tenuilaminaris* (Sollas, 1886)] (Van Soest et al. 2010).

Stelletta solida Tanita, 1963 is a secondary junior homonym of *Stelletta solida* (De Laubenfels, 1936). The latter was originally described as *Najax solida* De Laubenfels, 1936, but its suggested current generic affinity to *Stelletta* is uncertain (Van Soest, personal communication). Therefore, proposal of a new replacement name for the former is suspended here.

Haliclona digitata Tanita and Hoshino, 1989 is a secondary junior homonym of *Haliclona digitata* (Carter, 1882), *Haliclona digitata* (Lendenfeld, 1887), *Haliclona digitata* (Baer, 1906), and *Haliclona digitata* (Koltun, 1958). Because their generic affinities are uncertain at this moment, taking nomenclatural actions for these names should be deferred in the meantime.

Haliclona punctata Hoshino, 1981 (type locality, Ariake Sea, Japan) is a primary junior homonym of *Haliclona punctata* Bergquist and Warne, 1980 (type locality, Christchurch, New Zealand). The spicule lengths can be classified into two groups in the former, whereas the latter has almost uniform spicule length. As these are

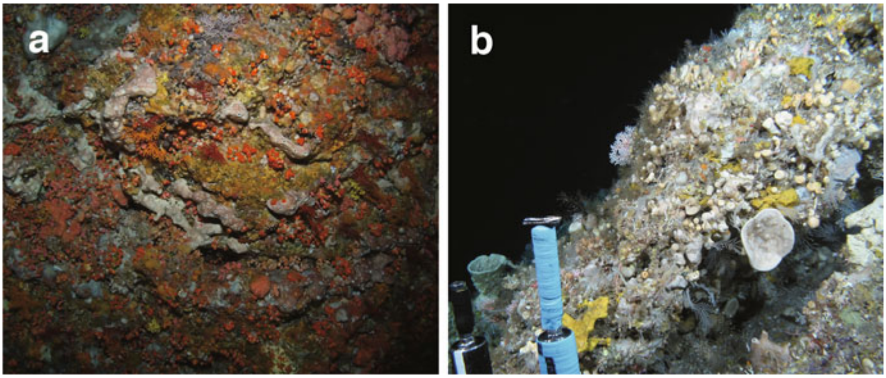

Fig. 13.2 Huge diversity of sponges from underside of overhang of Hachijo Island (**a**), 15 m deep, and Oshima-Shinsone seamount (**b**), southern Japan, ~200 m deep. (Photograh by ROV *Hyper-Dolphin*, JAMSTEC)

apparently different species, *Haliclona hoshinoi* nom. nov. is herein proposed to replace *Haliclona punctata* Hoshino, 1981.

13.3 Conclusion

A total of 636 species plus 16 subspecies of sponges are currently reported from Japanese waters, including all 4 classes of the phylum Porifera. Demosponges (class Demospongiae) are the most predominant and harbor 434 species, followed by calcareous sponges (class Calcarea, 119 spp.), hexactinellid or glass sponges (class Hexactinellida, 78 spp.), and homoscleromorph sponges (class Homoscleromorpha, 5 spp.). However, the number of species is still underestimated considering the diversity of marine habitat around Japan (Fujikura et al. 2010). By adding sponge fauna from the southern part of Japan (Fig. 13.2a), seamounts (Fig. 13.2b), and soft-bodied or thinly encrusting species living in both shallow and deep waters around Japan, the number of species is expected to be at least double.

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Appendix

A list of all sponge species recorded from Japan

Phylum Porifera Grant, 1836
Class Homoscleromorpha Bergquist, 1978
Order Homosclerophorida Dendy, 1905
Family Plakinidae Schulze, 1880
Genus *Plakina* Schulze, 1880
Plakina monolopha Schulze, 1880
Plakina tetralophoides Muricy et al., 1998
Genus *Plakortis* Schulzer, 1880
Plakortis japonica (Hoshino, 1977)
Plakortis lita de Laubenfels, 1954
Plakortis simplex Schulze, 1880
Class Calcarea Bowerbank, 1862
Subclass Calcaronea Bidder, 1898
Order Baerida Borojevic, Boury-Esnault & Vacelet, 2000
Family Baeriidae Borojevic, Boury-Esnault & Vacelet, 2000
Genus *Leuconia* Grant, 1833
Leuconia dura (Hôzawa, 1929)
Family Trichogypsiidae Borojevic, Boury-Esnault & Vacelet, 2000
Genus *Leucyssa* Haeckel, 1872
Leucyssa spongilla Haeckel, 1872
Order Leucosolenida Hartman, 1958
Family Amphoriscidae Dendy, 1893
Genus *Leucilla* Haeckel, 1872
Leucilla hirsuta Tanita, 1942
Leucilla minuta Tanita, 1941
Family Grantiidae Dendy, 1893
Genus *Grantia* Fleming, 1828
Grantia cupula (Haeckel, 1872)
Grantia glabra Hôzawa, 1933
Grantia harai Hôzawa, 1929
Grantia kujiensis Hôzawa, 1933
Grantia nipponica Hôzawa, 1918
Grantia stylata Hôzawa, 1929
Grantia uchidai Hôzawa & Tanita, 1941
Genus *Leucandra* Haeckel, 1872
Leucandra abratsbo Hôzawa, 1929
Leucandra amakusana Tanita, 1943
Leucandra cerebrum Hôzawa & Tanita, 1941
Leucandra foliata Hôzawa, 1918
Leucandra fragilis Hôzawa, 1940
Leucandra glabra Hôzawa, 1940

(continued)

Leucandra globosa Tanita, 1943
Leucandra Hôzawai Tanita, 1942
Leucandra impigra Tanita, 1942
Leucandra kagoshimensis Hôzawa, 1929
Leucandra magna Tanita, 1942
Leucandra mediocancellata Hôzawa, 1940
Leucandra mitsukurii Hôzawa, 1929
Leucandra multituba Hôzawa, 1929
Leucandra nakamurai Tanita, 1942
Leucandra odawarensis Hôzawa, 1929
Leucandra okinoseana Hôzawa, 1929
Leucandra onigaseana Hôzawa, 1929
Leucandra pacifica Hôzawa, 1929
Leucandra paucispina Hôzawa, 1929
Leucandra rigida Hôzawa, 1940
Leucandra sagmiana Hôzawa, 1929
Leucandra sola Tanita, 1942
Leucandra solida Hôzawa, 1929
Leucandra spinosa Hôzawa, 1940
Leucandra tomentosa Tanita, 1940
Leucandra tuba Hôzawa, 1918
Leucandra tuberculata Hôzawa, 1929
Leucandra valida Lambe, 1900
Leucandra vermiformis Tanita, 1941
Leucandra yuriagensis Hôzawa, 1933
Genus *Paragrantia* Hôzawa, 1940
Paragrantia waguensis Hôzawa, 1940
Genus *Ute* Schmidt, 1862
Ute armata Hôzawa, 1929
Ute pedunculata Hôzawa, 1929
Family Heteropiidae Dendy, 1893
Genus *Grantessa* Lendenfeld, 1885
Grantessa ampullae Hôzawa, 1940
Grantessa basipapillata Hôzawa, 1916
Grantessa intusarticulata (Carter, 1886)
Grantessa mitsukurii Hôzawa, 1916
Grantessa nemurensis Hôzawa, 1929
Grantessa parva Tanita, 1942
Grantessa sagamiana Hôzawa, 1916
Grantessa shimeji Hôzawa, 1916
Grantessa shimoda Tanita, 1942
Genus *Heteropia* Carter, 1886
Heteropia striata Hôzawa, 1916
Genus *Paraheteropia* Borojevic, 1965

(continued)

        - *Paraheteropia ijimai* (Hôzawa, 1916)
    - Genus *Vosmaeropsis* Dendy, 1893
        - *Vosmaeropsis grisea* Tanita, 1939
        - *Vosmaeropsis japonica* Hôzawa, 1929
        - *Vosmaeropsis maculata* Hôzawa, 1929
        - *Vosmaeropsis sasakii* Hôzawa, 1929
- Family Lelapiidae Dendy & Row, 1913
    - Genus *Pralelapia* Hôzawa, 1923
        - *Paralelapia nipponica* (Hara, 1894)
- Family Leucosoleniidae Minchin, 1900
    - Genus *Leucosolenia* Bowerbank, 1864
        - *Leucosolenia australis* Brøndsted, 1931
        - *Leucosolenia fragilis* (Haeckel, 1870)
        - *Leucosolenia minuta* Tanita, 1943
        - *Leucosolenia mollis* Tanita, 1941
        - *Leucosolenia pyriformis* Tanita, 1943
        - *Leucosolenia serica* Tanita, 1942
        - *Leucosolenia eleanor* Urban, 1906
        - *Leucosolenia tenera* Tanita, 1940
        - *Leucosolenia ventosa* Hôzawa, 1940
- Family Sycettidae Dendy, 1893
    - Genus *Sycetta* Haeckel, 1872
        - *Sycetta conifera* (Haeckel, 1870)
        - *Sycetta quadriradiata* Hôzawa, 1929
    - Genus *Sycon* Risso, 1827
        - *Sycon album* Tanita, 1942
        - *Sycon calcaravis* Hôzawa, 1929
        - *Sycon ciliatum* (Fabricius, 1780)
        - *Sycon cylindricum* Tanita, 1942
        - *Sycon digitiforme* Hôzawa, 1929
        - *Sycon ensiferum* Dendy, 1893
        - *Sycon globulatum* Hôzawa, 1929
        - *Sycon lendenfeldi* Row & Hôzawa, 1931
        - *Sycon luteolum* Tanita, 1942
        - *Sycon matsushimense* Tanita, 1940
        - *Sycon misakiense* Hôzawa, 1929
        - *Sycon mundulum* Lambe, 1900
        - *Sycon okadai* Hôzawa, 1929
        - *Sycon ornatum* Kirk, 1898
        - *Sycon pulchrum* Tanita, 1943
        - *Sycon raphanus* Schmidt, 1862
        - *Sycon rotundum* Tanita, 1941
        - Sycon satsumense Hôzawa, 1929
        - *Sycon urugamii* Tanita, 1940

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Sycon simushirense Hôzawa, 1918
Sycon yatsui Hôzawa, 1929
Order Lithonida Vacelet, 1981
Family Minchinellidae Dendy & Row, 1913
Genus *Petrostroma* Döderlein, 1892
Petrostroma schulzei Döderlein, 1892
Subclass Calcinea Bidder, 1898
Order Clathrinida Hartman, 1958
Family Clathrinidae Minchin, 1900
Genus *Arthuria* Klautau et al., 2013
Arthuria canariensis (Miklucho-Maclay, 1868)
Genus *Clathria* Gray, 1867
Clathrina coriacea (Montagu, 1814)
Clathrina gardineri (Dendy, 1913)
Clathrina izuensis (Tanita, 1942)
Clathrina laxa (Kirk, 1896)
Clathrina mutsu (Hôzawa, 1928)
Clathrina primordialis (Haeckel, 1872)
Clathrina stipitata (Dendy, 1891)
Clathrina soyo (Hôzawa, 1933)
Genus *Ernstia* Klautau et al., 2013
Ernstia sagamiana (Hôzawa, 1929)
Genus *Guancha* Miklucho-Maclay, 1868
Guancha blanca Miklucho-Maclay, 1868
Family Dendyidae de Laubenfels, 1936
Genus *Dendya* Bidder, 1898
Dendya clathrata (Carter, 1883)
Dendya quadripodifera Hôzawa, 1929
Dendya triradiata Tanita, 1943
Genus *Soleniscus* Borojevic, Boury-Esnault & Vacelet, 1990
Soleneiscus japonicus (Haeckel, 1872)
Family Leucaltidae Dendy & Row, 1913
Genus *Ascandra* Haeckel, 1872
Ascandra atlantica (Thacker, 1908)
Genus *Leucaltis* Haeckel, 1872
Leucaltis clathria Haeckel, 1872
Leucaltis tenuis Hôzawa, 1929
Family Leucascidae Dendy, 1893
Genus *Ascaltis* Haeckel, 1872
Ascaltis depressa (Dendy, 1891)
Ascaltis reticulum (Schmidt, 1862)
Ascaltis wilsoni (Dendy, 1891)
Genus *Ascoleucetta* Dendy & Frederick, 1924
Ascoleucetta amitsba (Hôzawa, 1929)

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Genus *Leucascus* Dendy, 1892
Leucascus protogenes (Haeckel, 1872 sensu Dendy, 1891)
Family Leucettidae de Laubenfels, 1936
Genus *Leucetta* Haeckel, 1872
Leucetta chagosensis Dendy, 1913
Leucetta pyriformis Dendy, 1913
Class Hexactinellida Schmidt, 1870
Subclass Amphidiscophora Schulze, 1886
Order Amphidiscosida Schrammen, 1924
Family Hyalonematidae Gray, 1857
Genus *Hyalonema* Gray, 1832
Hyalonema (*Corynonema*) *clathratum* Ijima, 1895
Hyalonema (*Corynonema*) *owstoni* Ijima, 1894
Hyalonema (*Coscinonema*) *kirkpatricki* Ijima, 1927
Hyalonema (*Coscinonema*) *ovatum* Okada, 1932
Hyalonema (*Cyliconema*) *apertum* Schulze, 1886
Hyalonema (*Cyliconema*) *hozawai* Okada, 1932
Hyalonema (*Cyliconema*) *ovatum* Ijima, 1895
Hyalonema (*Hyalonema*) *pellucidum* Ijima, 1894
Hyalonema (*Hyalonema*) *sieboldii* Gray, 1835
Family Pheronematidae Gray, 1870
Genus *Pheronema* Leidy, 1868
Pheronema giganteum Schulze, 1886
Pheronema globosum Schulze, 1886
Pheronema globosum kagoshimensis Okada, 1932
Pheronema ijimai Okada, 1932
Pheronema surugense Okada, 1932
Genus *Semprella* Gray, 1868
Semperella schultzei (Semper, 1868)
Semperella stomata Ijima, 1896
Genus *Sericolophus* Ijima, 1901
Sericolophus reflexus (Ijima, 1894)
Subclass Hexasterophora Schulze, 1886
Order Hexactinosida Schrammen, 1912
Suborder Sceptrulophora Mehl, 1992
Family Aphrocallistidae Gray, 1867
Genus *Aphrocallistes* Gray, 1858
Aphrocallistes beatrix Gray, 1858
Aphrocallistes beatrix beatrix Gray, 1858
Aphrocallistes beatrix orientalis Ijima, 1916
Aphrocallistes vastus Schulze, 1886
Genus *Heterochone* Ijima 1927
Heterochone calyx (Schulze, 1886)
Family Euretidae Zittel, 1877

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Subfamily Chonelasmatinae Schrammen, 1912
Genus *Chonelasma* Schulze, 1886
Chonelasma doederleini Schulze, 1886
Genus *Periphragella* Marshall, 1875
Periphragella elisae Marshall, 1875
Genus *Tretochone* Reid, 1958
Tretochone duplicata (Topsent, 1928)
Subfamily Euretinae Zittel, 1877
Genus *Calyptorete* Okada, 1925
Calyptorete ijimai Okada, 1925
Genus *Endorete* Topsent, 1928
Endorete pertusum Topsent, 1928
Genus *Eurete* Semper, 1868
Eurete bowerbanki Schulze, 1886
Eurete nipponicum Okada, 1932
Eurete sacculiforme Okada, 1932
Eurete schmidtii Schulze, 1886
Genus *Pararete* Ijima, 1927
Pararete carteri (Schulze, 1886)
Pararete farreopsis (Carter, 1877)
Family Farreidae Gray, 1872
Genus *Farrea* Bowerbank, 1862
Farrea occa Bowerbank, 1862
Farrea occa occa Bowerbank, 1862
Farrea sollasi Schulze, 1886
Farrea sollasi sollasi Schulze, 1886
Farrea sollasi yakushimensis Okada, 1932
Farrea vosmaeri Schulze, 1886
Family Tretodictylidae Schulze, 1886
Genus *Hexactinella* Carter, 1885
Hexactinella ventilabrum Carter, 1885
Genus *Tretodictyum* Schulze, 1886
Tretodictyum tubulosum Schulze, 1886
Order Lyssacinosida Zittel, 1877
Family Euplectellidae Gray, 1867
Subfamily Bolosominae Tabachnick, 2002
Genus *Bolosoma* Ijima, 1904
Bolosoma paradictyum (Ijima, 1903)
Subfamily Corbitellinae Gray, 1872
Genus *Regadrella* Schmidt, 1880
Regadrella komeyamai Ijima, 1901
Regadrella okinoseana Ijima, 1896
Genus *Walteria* Schulze, 1886
Walteria leuckarti Ijima, 1896

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Walteria leuckarti leuckarti Ijima, 1896
Subfamily Euplectellinae Gray, 1867
Genus *Euplectella* Owen, 1841
Euplectella aspergillum Owen, 1841
Euplectella curvistellata Ijima, 1901
Euplectella imperialis Ijima, 1894
Euplectella marshalli Ijima, 1895
Euplectella oweni Herklots & Marshall, 1868
Genus *Holascus* Schulze, 1886
Holascus belyaevi Koltun, 1970
Family Leucopsacidae Ijima, 1903
Genus *Chaunoplectella* Ijima, 1896
Chaunoplectella cavernosa Ijima, 1896
Genus *Leucopsacus* Ijima, 1898
Leucopsacus orthodocus Ijima, 1898
Leucopsacus scoliodocus Ijima, 1903
Leucopsacus scoliodocus var. *scoliodocus* Ijima, 1903
Genus *Oopsacas* Topsent, 1927
Oopsacas spinifera (Ijima, 1903)
Family Rossellidae Schulze, 1885
Subfamily Acanthascinae Schulze, 1897
Genus *Acanthascus* Schulze, 1886
Acanthascus alani Ijima, 1898
Acanthascus cactus Schulze, 1886
Acanthascus pachyderma Okada, 1932
Genus *Rhabdocalyptus* Schulze, 1886
Rhabdocalyptus bidentatus Okada, 1932
Rhabdocalyptus capillatus Ijima, 1897
Rhabdocalyptus mollis Schulze, 1886
Rhabdocalyptus unguiculatus Ijima, 1904
Rhabdocalyptus victor Ijima, 1897
Genus *Staurocalyptus* Ijima, 1897
Staurocalyptus affinis Ijima, 1904
Staurocalyptus entacanthus Ijima, 1904
Staurocalyptus glaber Ijima, 1897
Staurocalyptus heteractinus Ijima, 1897
Staurocalyptus microchetus Ijima, 1898
Staurocalyptus pleorhaphides Ijima, 1897
Staurocalyptus tubulosus Ijima, 1904
Subfamily Lanuginellinae Gray, 1872
Genus *Caulophacus* Schulze, 1886
Caulophacus (*Caulodiscus*) *lotifolium* Ijima, 1903
Caulophacus (*Caulophacus*) *elegans* Schulze, 1886
Genus *Lanuginella* Schmidt, 1870

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Lanuginella pupa Schmidt, 1870
Genus *Sympagella* Schmidt, 1870
Sympagella anomala Ijima, 1903
Subfamily Rossellinae Schulze, 1885
Genus *Aulosaccus* Ijima, 1896
Aulosaccus mitsukuri Ijima, 1898
Aulosaccus schulzei Ijima, 1896
Genus *Crateromorpha* Gray in Carter, 1872
Crateromorpha (*Crateromorpha*) *meyeri* Gray, 1872
Crateromorpha (*Crateromorpha*) *meyeri corrugata* Ijima, 1898
Crateromorpha (*Crateromorpha*) *meyeri rugosa* Ijima, 1898
Crateromorpha (*Crateromorpha*) *meyeri tuberosa* Ijima, 1898
Crateromorpha (*Crateromorpha*) *pachyactina* Ijima, 1898
Genus *Hyalascus* Ijima, 1896
Hyalascus giganteus Ijima, 1898
Hyalascus sagamiensis Ijima, 1896
Hyalascus similis Ijima, 1904
Genus *Scyphidium* Schulze, 1900
Scyphidium longispinum (Ijima, 1896)
Scyphidium namiyei (Ijima, 1898)
Genus *Vitrollula* Ijima, 1898
Vitrollula fertilis Ijima, 1898
Class Demospongiae Sollas, 1885
Subclass Verongimorpha Erpenbeck et al., 2012
Order Chondrosiida Boury-Esnault & Lopes, 1985
Family Chondrosiidae Schulze, 1877
Genus *Chondrosia* Nardo, 1847
Chondrosia reniformis Nardo, 1847
Order Chondrillida Redmond *et al.*, 2013
Family Chondrillidae Gray, 1872
Genus *Chondrilla* Schmidt, 1862
Chondrilla australiensis Carter, 1873
Chondrilla oxyastera Tanita & Hoshino, 1989
Subclass Keratosa Grant, 1861
Order Dendroceratida Minchin, 1900
Family Darwinellidae Merejkowsky, 1879
Genus *Dendrilla* Lendenfeld, 1883
Dendrilla cactos (Selenka, 1867)
Order Dictyoceratida Minchin, 1900
Family Dysideidae Gray, 1867
Genus *Dysidea* Johnston, 1842
Dysidea fragilis (Montagu, 1814)
Dysidea minna Hoshino, 1985
Dysidea variabilis (Duchassaing & Michelotti, 1864)

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Genus *Euryspongia* Row, 1911
Euryspongia lobata Bergquist, 1965
Genus *Lamellodysidea* Cook & Bergquist, 2002
Lamellodysidea herbacea (Keller, 1889)
Family Ircinidae Gray, 1867
Genus *Ircinia* Nardo, 1833
Ircinia collectrix (Poléjaeff, 1884)
Ircinia strobilina (Lamarck, 1816)
Genus *Sarcotragus* Schmidt, 1862
Sarcotragus fasciculatus (Pallas, 1766)
Family Spongiidae Gray, 1867
Genus *Hippospongia* Schulze, 1879
Hippospongia communis (Lamarck, 1814)
Genus *Hyattella* Lendenfeld, 1888
Hyattella cribriformis (Hyatt, 1877)
Hyattella intestinalis (Lamarck, 1814)
Genus *Spongia* Linnaeus, 1759
Spongia (*Spongia*) *hispida* Lamarck, 1814
Spongia (*Spongia*) *officinalis* Linnaeus, 1759
Spongia (*Spongia*) *zimocca* Schmidt, 1862
Family Thorectidae Bergquist, 1978
Subfamily Phyllospongiindae Keller, 1889
Genus *Phyllospongia* Ehlers, 1870
Phyllospongia lamellosa (Esper, 1794)
Subfamily Thorectinae Bergquist, 1978
Genus *Aplysinopsis* Lendenfeld, 1888
Aplysinopsis elegans Lendenfeld, 1888
Genus *Hyrtios* Duchassaing & Michelotti, 1864
Hyrtios erectus (Keller, 1889)
Genus *Scalariospongia* Cook & Bergquist, 2000
Scalarispongia scalaris (Schmidt, 1862)
Genus *Smenospongia* Wiedenmayer, 1977
Smenospongia cf. *echina* (de Laubenfels, 1934)
Genus *Thorectandra* Lendenfeld, 1889
Thorectandra boletus (Lamarck, 1815)
Subclass Heteroscleromorpha Cárdenas, Perez & Boury-Esnault, 2012
Order Haplosclerida Topsent, 1928
Family Callyspongiidae de Laubenfels, 1936
Genus *Callyspongia* Duchassaing & Michelotti, 1864
Callyspongia (*Callyspongia*) *differentiata* (Dendy, 1922)
Callyspongia (*Callyspongia*) *fallax* Duchassaing & Michelotti, 1864
Callyspongia (*Callyspongia*) *ramosa* (Gray, 1843)
Callyspongia (*Callyspongia*) *serpentina* (Lamarck, 1814)
Callyspongia (*Cladochalina*) *diffusa* (Ridley, 1884)

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Callyspongia (*Cladochalina*) *fibrosa* (Ridley & Dendy, 1886)
Callyspongia (*Cladochalina*) *pergamentacea* (Ridley, 1881)
Callyspongia (*Cladochalina*) *rautenfeldi* (Topsent, 1928)
Callyspongia (*Cladochalina*) *subarmigera* (Ridley, 1884)
Callyspongia (*Cladochalina*) *vaginalis* (Lamarck, 1814)
Callyspongia (*Toxochalina*) *robusta* (Ridley, 1884)
Callyspongia ariakensis Tanita, 1968
Callyspongia bispicula Tanita, 1961
Callyspongia confoederata (sensu Ridley, 1884)
Callyspongia ecklonia Hoshino, 1981
Callyspongia elegans (sensu Thiele, 1899)
Callyspongia flabelliformis Tanita, 1968
Callyspongia murex Hoshino, 1981
Callyspongia patula Hoshino, 1981
Callyspongia poculum (Carter, 1885)
Callyspongia sphaericuslobata (Hoshino, 1981)
Callyspongia taupea (Tanita & Hoshino, 1989)
Callyspongia truncata (Lindgren, 1897)
Callyspongia waguensis Tanita, 1961
Family Chalinidae Gray, 1867
Genus *Chalinula* Schmidt, 1868
Chalinula loosanoffi (Hartman, 1958)
Genus *Haliclona* Grant, 1936
Haliclona (*Gellius*) *cymaeformis* (Esper, 1794)
Haliclona (*Gellius*) *fibulata* (Schmidt, 1862)
Haliclona (*Gellius*) *primitiva* (Lundbeck, 1902)
Haliclona (*Gellius*) *strongylata* (Lindgren, 1897)
Haliclona (*Haliclona*) *oculata* (Linnaeus, 1759)
Haliclona (*Haliclona*) *ramosamassa* Hoshino, 1981
Haliclona (*Reniera*) *aquaeductus* (Schmidt, 1862)
Haliclona (*Reniera*) *cinerea* (Grant, 1826)
Haliclona (*Reniera*) *clathrata* (Dendy, 1895)
Haliclona (*Reniera*) *negro* (Tanita, 1965)
Haliclona bucina Tanita & Hoshino, 1989
Haliclona cylindrica (Tanita, 1961)
Haliclona densaspicula Hoshino, 1981
Haliclona digitata Tanita & Hoshino, 1989
Haliclona ellipsis Hoshino, 1981
Haliclona enormismacula Hoshino, 1981
Haliclona frondosa Hoshino, 1981
Haliclona hoshinoi **nom. nov.**
Haliclona hydroida Tanita & Hoshino, 1989
Haliclona lentus Hoshino, 1981
Haliclona liber (Hoshino, 1981)

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Haliclona nishimurai Tanita, 1977
Haliclona offerospicula Hoshino, 1981
Haliclona onomichiensis Hoshino, 1981
Haliclona permollis (Bowerbank, 1866)
Haliclona permollisimilis Hoshino, 1981
Haliclona pigmentifera (Dendy, 1905)
Haliclona rectangularis (Ridley & Dendy, 1886)
Haliclona robustaspicula Hoshino, 1981
Haliclona sasajimensis Hoshino, 1981
Haliclona sataensis Hoshino, 1981
Haliclona scabritia Tanita & Hoshino, 1989
Haliclona shimoebuensis (Hoshino, 1981)
Haliclona sortitio Hoshino, 1981
Haliclona surrufa Hoshino, 1981
Haliclona tachibanaensis Hoshino, 1981
Haliclona tenuis Hoshino, 1981
Haliclona tenuispiculata Burton, 1934
Haliclona uwaensis Hoshino, 1981
Haliclona viola Hoshino, 1981
Haliclona violapurpura Hoshino, 1981
Family Niphatidae van Soest, 1980
Genus *Amphimedon* Duchassaing & Michelotti, 1864
Amphimedon aitsuensis (Hoshino, 1981)
Amphimedon complanata (Duchassaing, 1850)
Genus *Gelliodes* Ridley, 1884
Gelliodes callista de Laubenfels, 1954
Genus *Hemigellius* Burton, 1932
Hemigellius duosigmata Tanita & Hoshino, 1989
Hemigellius izuensis (Hoshino, 1982)
Genus *Niphates* Duchassaing & Michelotti, 1864
Niphates obtusispiculifera (Dendy, 1905)
Family Petrosiidae van Soest, 1980
Genus *Neopetrosia* de Laubenfels, 1949
Neopetrosia carbonaria (Lamarck, 1814)
Neopetrosia similis (Ridley & Dendy, 1886)
Neopetrosia tuberosa (Dendy, 1922)
Genus *Petrosia* Vosmaer, 1885
Petrosia (*Petrosia*) *solida* Hoshino, 1981
Petrosia (*Petrosia*) *solusstrongyla* Hoshino, 1981
Petrosia (*Petrosia*) *spheroida* Tanita, 1967
Petrosia (*Petrosia*) *ushitsuensis* Tanita, 1963
Petrosia (*Petrosia*) *volcano* Hoshino, 1976
Petrosia (*Strongylophora*) *corticata* (Wilson, 1925)
Petrosia (*Strongylophora*) *mauritiana* (Carter, 1885)

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Genus *Xestospongia* de Laubenfels, 1932
Xestospongia testudinaria (Lamarck, 1815)
Family Phloeodictyidae Carter, 1882
Genus *Oceanapia* Norman, 1869
Oceanapia ooita (Hoshino, 1981)
Oceanapia toxonisimilis (Hoshino, 1981)
Order Spongillida Manconi & Pronzato, 2002
Family Spongillidae Gray, 1867
Genus *Ephydatia* Lamouroux, 1816
Ephydatia fluviatilis (Linnaeus, 1759)
Ephydatia fortis Weltner, 1895
Ephydatia muelleri (Lieberkühn, 1856)
Ephydatia japonica (Hilgendorf, 1882)
Genus *Eunapius* Gray, 1867
Eunapius conifer (Annandale, 1916)
Eunapius fragilis (Leidy, 1851)
Eunapius sinensis (Annandale, 1910)
Eunapius ryuensis (Sasaki, 1970)
Genus *Heteromeyenia* Potts, 1881
Heteromeyenia stepanowii (Dybowski, 1884)
Genus *Heterorotula* Penney & Racek, 1968
Heterorotula multidentata (Weltner, 1895)
Genus *Pectispongilla* Annandale, 1909
Pectispongilla subspinosa Annandale, 1911
Genus *Pottsiela* Volkmer-Ribeiro et al., 2010
Pottsiela inarmata (Annandale, 1918)
Genus *Radiospongilla* Penney & Racek, 1968
Radiospongilla cerebellata (Bowerbank, 1863)
Radiospongilla crateriformis (Potts, 1882)
Radiospongilla sendai (Sasaki, 1936)
Radiospongilla hozawai (Sasaki, 1936)
Genus *Sanidastra* Volkmer-Ribeiro & Watanabe, 1983
Sanidastra yokotonensis Volkmer & Watanabe, 1983
Genus *Spongilla* Lamarck, 1816
Spongilla alba Carter, 1849
Spongilla lacustris (Linnaeus, 1759)
Spongilla shikaribensis Sasaki, 1934
Genus *Stratospongilla* Annandale, 1909
Stratospongilla akanensis (Sasaki, 1934)
Stratospongilla clementis (Annandale, 1909)
Genus *Trochospongilla* Vejdovsky, 1888
Trochospongilla latouchiana Annandale, 1907
Trochospongilla pennsylvanica (Potts, 1882)
Trochospongilla philottiana Annandale, 1907

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Genus *Umborotula* Penney & Racek, 1968
Umborotula bogorensis (Weber, 1890)
Order Scopalinida Morrow & Cárdenas, 2015
Family Scopalinidae Morrow et al., 2012
Genus *Stylissa* Hallmann, 1914
Stylissa massa (Carter, 1887)
Order Axinellida Lévi, 1953
Family Axinellidae Carter, 1875
Genus *Auletta* Schmidt, 1870
Auletta consimilis Thiele, 1898
Auletta halichondroides Thiele, 1898
Genus *Axinella* Schmidt, 1862
Axinella amorpha Tanita & Hoshino, 1989
Axinella convexa Hoshino, 1981
Axinella copiosa Thiele, 1898
Axinella cylindratus Hoshino, 1981
Axinella incrustans Thiele, 1898
Axinella infundibuliformis (Linnaeus, 1759)
Axinella profunda Ridley & Dendy, 1886
Axinella profunda var. *kurushima* Tanita, 1961
Axinella tenuis Thiele, 1898
Genus *Phakellia* Bowerbank, 1862
Phakellia elegans Thiele, 1898
Phakellia foliacea Thiele, 1898
Phakellia fusca Thiele, 1898
Phakellia izuensis Tanita & Hoshino, 1989
Phakellia paupera Thiele, 1898
Phakellia perforata Thiele, 1898
Phakellia pygmaea Thiele, 1898
Phakellia radiata (Dendy, 1916)
Genus *Reniochalina* Lendenfeld, 1888
Reniochalina stalagmitis Lendenfeld, 1888
Family Heteroxyidae Dendy, 1905
Genus *Negombo* Dendy, 1905
Negombo acanthosanidastera (Hoshino, 1981)
Negombo jogashimensis (Tanita & Hoshino, 1990)
Family Raspailliidae Nardo, 1833
Subfamily Thrinacophorinae Hooper, 2002
Genus *Ceratopsion* Strand, 1928
Ceratopsion clavatum (Thiele, 1898)
Ceratopsion erectum (Thiele, 1898)
Ceratopsion expansum (Thiele, 1898)
Ceratopsion ramosum (Thiele, 1898)
Subfamily Raspaillinae Nardo, 1833

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Genus *Aulospongus* Norman, 1878
Aulospongus villosus (Thiele, 1898)
Genus *Eurypon* Gray, 1867
Eurypon duoacanthostyla (Hoshino, 1981)
Eurypon inuisitatiacanthostyla (Hoshino, 1981)
Genus *Raspailia* Nardo, 1833
Raspailia folium Thiele, 1898
Raspailia hirsuta Thiele, 1898
Raspailia kasumiensis Tanita, 1965
Raspailia microacanthoxea Hoshino, 1976
Raspailia trachystyla Tanita, 1968
Order Bubarida Morrow & Cárdenas, 2015
Family Dictyonellidae van Soest, Diaz & Pomponi, 1990
Genus *Acanthella* Schmidt, 1862
Acanthella aculeata Thiele, 1898
Acanthella aculeata var. inconspicua Thiele, 1898
Acanthella dendyi (Bergquist, 1970)
Acanthella flabellata (Tanita, 1961)
Acanthella insignis Thiele, 1898
Acanthella minuta Tanita, 1968
Acanthella oviforma Tanita & Hoshino, 1989
Acanthella simplex Thiele, 1898
Acanthella styloida Tanita & Hoshino, 1989
Acanthella vulgata Thiele, 1898
Genus *Lipastrotethya* de Laubenfels, 1954
Lipastrotethya hilgendorfi (Thiele, 1898)
Order Biemnida Morrow, 2013
Family Biemnidae Hentschel, 1923
Genus *Biemna* Gray, 1867
Biemna rhabderemioides Bergquist, 1961
Biemna tetraphis Tanita & Hoshino, 1989
Order Tetractinellida Marshall, 1876
Suborder Astrophorina Sollas, 1887
Family Ancorinidae Schmidt, 1870
Genus *Asteropus* Sollas, 1888
Asteropus simplex (Carter, 1879)
Genus *Dercitus* Gray, 1867
Dercitus (*Halinastra*) *japonensis* van Soest, Beglinger & de Voogd, 2010
Genus *Jaspis* Gray, 1867
Jaspis duosaster Hoshino, 1981
Jaspis hiwasaensis Hoshino, 1987
Jaspis sadoensis Tanita, 1965
Jaspis stellifera (Carter, 1879)
Genus *Stelletta* Schmidt, 1862

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Stelletta atrophia Hoshino, 1981
Stelletta freitasi Lévi, 1964
*Stelletta gigante*a Tanita, 1965
Stelletta grubii Schmidt, 1862
Stelletta japonica Lebwohl, 1914
Stelletta maxima Thiele, 1898
Stelletta misakensis Lebwohl, 1914
Stelletta morikawai Tanita, 1961
Stelletta naseana Thiele, 1898
Stelletta orientalis Thiele, 1898
Stelletta orthotriaena Koltun, 1966
Stelletta ovalae Tanita, 1965
Stelletta pisum Thiele, 1898
Stelletta purpurea Ridley, 1884
Stelletta solida sensu Tanita, 1963
Stelletta splendens Tanita, 1965
Stelletta subtilis (Sollas, 1886)
Stelletta teres Lebwohl, 1914
Stelletta tuba Lebwohl, 1914
Stelletta tetrafurcata Hoshino, 1981
Stelletta validissima Thiele, 1898
Family Geodiidae Gray, 1867
Subfamily Erylinae Sollas, 1888
Genus *Caminella* Lendenfeld, 1894
Caminella velata Lebwohl, 1914
Genus *Caminus* Schmidt, 1862
Caminus awashimensis Tanita, 1969
Caminus strongyla (Hoshino, 1981)
Genus *Erylus* Gray, 1867
Erylus placenta Thiele, 1898
Genus *Penares* Gray, 1867
Penares hilgendorfi (Thiele, 1898)
Penares incrustans Tanita, 1963
Penares metastrosa (Lebwohl, 1914)
Subfamily Geodiinae Sollas, 1888
Genus *Geodia* Lamarck, 1815
Geodia amadaiba Tanita & Hoshino, 1989
Geodia cylindrica Thiele, 1898
Geodia exigua Thiele, 1898
Geodia hilgendorfi Thiele, 1898
Geodia hilgendorfi granosa Lendenfeld, 1910
Geodia hyotania (Tanita, 1965)
Geodia japonica (Sollas, 1888)
Geodia lendenfeldi Stone, Lehnert & Reiswig, 2011

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Geodia obscura (Thiele, 1898)
Geodia orthomesotriaena Lebwohl, 1914
Geodia reniformis Thiele, 1898
Geodia reniformis var. *robusta* Lebwohl, 1914
Geodia variospiculosa Thiele, 1898
Geodia variospiculosa var. *aapta* Lebwohl, 1914
Geodia variospiculosa clavigera Lendenfeld, 1910
Geodia variospiculosa intermedia Lendenfeld, 1910
Geodia variospiculosa micraster Lendenfeld, 1910
Geodia velata (Lebwohl, 1914)
Family Pachastrellidae Carter, 1875
Genus *Characella* Sollas, 1886
Characella ijimai (Lebwohl, 1914)
Characella laevis Lebwohl, 1914
Characella rericulata Lebwohl, 1914
Characella stellettodes (Carter, 1885)
Genus *Pachastrella* Schmidt, 1868
Pachastrella cribrum Lebwohl, 1914
Pachastrella fusca Lebwohl, 1914
Pachastrella loricata (Lebwohl, 1914) taxon inquirendum
Pachastrella scrobiculosa Lebwohl, 1914
Genus *Triptolemma* de Laubenfels, 1955
Triptolemma strongylata Bertolino et al., 2011
Family Theneidae Carter, 1883
Genus *Thenea* Gray, 1867
Thenea calyx Thiele, 1898
Thenea compacta Thiele, 1898
Thenea compressa Thiele, 1898
Thenea grayi Sollas, 1886
Thenea grayi var. *lateralis* Thiele, 1898
Thenea grayi var. *grayi* Sollas, 1886
Thenea hemisphaerica Thiele, 1898
Thenea irregularis Thiele, 1898
Thenea nucula Thiele, 1898
Thenea shimodensis Hoshino, 1982
Family Theonellidae Lendenfeld, 1903
Genus *Discodermia* du Bocage, 1869
Discodermia calyx Döderlein, 1884
Discodermia emarginata Dendy, 1905
Discodermia irregularis Hoshino, 1976
Discodermia japonica Döderlein, 1884
Discodermia jogashima Tanita & Hoshino, 1989
Discodermia kiiensis Hoshino, 1977
Discodermia vermicularis Döderlein, 1884

(continued)

Genus *Silquariaspongia* Hoshino, 1981
Siliquariaspongia japonica Hoshino, 1981
Genus *Theonella* Gray, 1868
Theonella swinhoei Gray, 1868
Family Thoosidae Cockerell, 1925
Genus *Alectona* Carter, 1879
Alectona verticillata (Johnson, 1899)
Alectona sarai Calcinai *et al*., 2008
Alectona sorrentini Bavestrello *et al*., 1998
Alectona triradiata Lévi & Lévi, 1983
Alectona wallichii (Carter, 1874)
Family Vulcanellidae Cárdenas et al., 2011
Genus *Poecillastra* Sollas, 1888
Poecillastra japonica (Thiele, 1898)
Poecillastra tenuilaminaris (Sollas, 1886)
Genus *Vulcanella* Sollas, 1886
Vulcanella acanthoxea (Tanita & Hoshino, 1989)
Vulcanella cribriporosa (Lebwohl, 1914)
Vulcanella doederleini (Thiele, 1898)
Vulcanella netheides (Lebwohl, 1914)
Vulcanella porosa (Lebwohl, 1914)
Suborder Spirophorina Bergquist & Hogg, 1969
Family Scleritodermidae Sollas, 1888
Genus *Microscleroderma* Kirkpatrick, 1903
Microscleroderma chonelleides (Döderlein, 1884)
Family Tetillidae Sollas, 1886
Genus *Cinachyrella* Wilson, 1925
Cinachyrella australiensis (Carter, 1886)
Genus *Craniella* Schmidt, 1870
Craniella cranium (Müller, 1776)
Craniella globosa Thiele, 1898
Craniella lentiformis Thiele, 1898
Craniella lentisimilis Tanita & Hoshino, 1989
Craniella ovata (Thiele, 1898)
Craniella prosperiaradix Tanita & Hoshino, 1989
Craniella serica (Lebwohl, 1914)
Craniella varians Thiele, 1898
Genus *Tetilla* Schmidt, 1868
Tetilla anamonaena (Tanita, 1968)
Tetilla ellipsoida (Hoshino, 1982)
Tetilla ginzan Tanita, 1965
Tetilla japonica Lampe, 1886
Order Agelasida Hartman, 1980
Family Agelasidae Verrill, 1907

(continued)

Genus *Agelas* Duchassaing & Michelotti, 1864
Agelas nakamurai Hoshino, 1985
Agelas nemoechinata Hoshino, 1985
Agelas robusta Pulitzer-Finali, 1982
Family Astroscleridae Lister, 1900
Genus *Astrosclera* Lister, 1900
Astrosclera willeyana Lister, 1900
Family Hymerhabdiidae Morrow et al., 2012
Genus *Prosuberites* Topsent, 1893
Prosuberites exiguus Thiele, 1898
Prosuberites inconspicuus Thiele, 1898
Prosuberites sagamensis Thiele, 1898
Order Polymastiida Morrow & Cárdenas, 2015
Family Polymastiidae Gray, 1867
Genus *Polymastia* Bowerbank, 1864
Polymastia affinis Thiele, 1898
Polymastia granulosa Brøndsted, 1924
Polymastia simplicissima Thiele, 1898
Genus *Quasillina* Norman, 1869
Quasillina brevis (Bowerbank, 1861)
Order Merliida Vacelet, 1979
Family Merliidae Kirkpatrick, 1908
Genus *Merlia* Kirkpatrick, 1908
Merlia tenuis Hoshino, 1990
Order Desmacellida Morrow & Cárdenas, 2015
Family Desmacellidae Ridley & Dendy, 1886
Genus *Desmacella* Schmidt, 1870
Desmacella infundibuliformis (Vosmaer, 1885)
Desmacella vagabunda Schmidt, 1870
Order Poecilosclerida Topsent, 1928
Family Acarnidae Dendy, 1922
Genus *Acarnus* Gray, 1867
Acarnus bicladotylotus Hoshino, 1981
Acarnus tener Tanita, 1963
Family Chondropsidae Carter, 1886
Genus *Batzella* Topsent, 1893
Batzella melanos (de Laubenfels, 1954)
Genus *Strongylacidon* Lendenfeld, 1897
Strongylacidon kaneohe (de Laubenfels, 1950)
Family Cladorhizidae Dendy, 1922
Genus *Abyssocladia* Lévi, 1964
Abyssocladia myojinensis Ise & Vacelet, 2010
Abyssocladia natushimae Ise & Vacelet, 2010
Genus *Chondrocladia* Thomson, 1873

(continued)

    - *Chondrocladia* (*Chondrocladia*) *magna* Tanita, 1965
    - *Chondrocladia* (*Chondrocladia*) *yatsui* Topsent, 1930
- Family Coelosphaeridae Dendy, 1922
  - Genus *Coelosphaera* Thomson, 1873
    - *Coelosphaera* (*Coelosphaera*) *calcifera* (Burton, 1934)
    - *Coelosphaera* (*Coelosphaera*) *crusta* Tanita & Hoshino, 1989
  - Genus *Forceptia* Carter, 1874
    - *Forcepia* (*Forcepia*) *solustylota* Hoshino 1977
    - *Forcepia* (*Forcepia*) *volsella* Topsent, 1928
  - Genus *Lissodendoryx* Topsent, 1892
    - *Lissodendoryx* (*Ectyodoryx*) *balanoides* (Koltun 1959)
    - *Lissodendoryx* (*Lissodendoryx*) *isodictyalis* (Carter, 1882)
    - *Lissodendoryx* (*Lissodendoryx*) *rarus* Hoshino, 1981
- Family Crellidae Dendy, 1922
  - Genus *Crella* Gray, 1867
    - *Crella incrustans incrustans* (Carter, 1885)
- Family Desmacididae Schmidt, 1870
  - Genus *Desmapsamma* Burton, 1934
    - *Desmapsamma anchorata* (Carter, 1882)
- Family Esperiopsidae Hentschel, 1923
  - Genus *Amphilectus* Vosmaer, 1880
    - *Amphilectus fucorum* (Esper, 1794)
    - *Amphilectus unciger* (Topsent, 1928)
  - Genus *Esperiopsis* Carter, 1882
    - *Esperiopsis plumosa* Tanita, 1965
    - *Esperiopsis variussigma* Hoshino, 1981
  - Genus *Semisuberites* Carter, 1877
    - *Semisuberites cribrosa* (Miklucho-Maclay, 1870)
- Family Guitarridae Dendy, 1924
  - Genus *Euchelipluma* Topsent, 1909
    - *Euchelipluma arbuscula* (Topsent, 1928)
  - Genus *Tetrapocillon* Brøndsted, 1924
    - *Tetrapocillon kurushimensis* Tanita, 1961
- Family Hymedesmiidae Topsent, 1928
  - Genus *Hymedesmia* Bowerbank, 1864
    - *Hymedesmia* (*Hymedesmia*) *procumbens* Lundbeck, 1910
    - *Hymedesmia* (*Hymedesmia*) *uchinourensis* Hoshino, 1981
  - Genus *Myxodoryx* Burton, 1929
    - *Myxodoryx jogashimensis* Tanita & Hoshino, 1989
  - Genus *Phorbas* Duchassaing & Michelotti, 1864
    - *Phorbas tanitai* Hajdu & Teixeira, 2011
    - *Phorbas tokushima* (Tanita, 1970)
- Family Iotrochotidae Dendy, 1922
  - Genus *Iotrochota* Ridley, 1884

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Iotrochota baculifera Ridley, 1884
Family Isodictyidae Dendy, 1924
Genus *Isodictya* Bowerbank, 1864
Isodictya palmata (Ellis & Solander, 1786)
Family Latunculiidae Topsent, 1922
Genus *Latuncullia* du Bocage, 1869
Latrunculia (*Latrunculia*) *ikematsui* Tanita, 1968
Family Microcionidae Carter, 1875
Subfamily Microcioninae Carter, 1875
Genus *Clathria* Schmidt, 1862
Clathria (*Clathria*) *acanthostyli* (Hoshino, 1981)
Clathria (*Clathria*) *productitoxa* (Hoshino, 1981)
Clathria (*Clathria*) *shirahama* Tanita, 1977
Clathria (*Clathria*) *spinispicula* Tanita, 1968
Clathria (*Microciona*) *spinatoxa* (Hoshino, 1981)
Clathria (*Thalysias*) *fasciculata* Wilson, 1925
Clathria (*Thalysias*) *naikaiensis* (Hoshino, 1981)
Clathria (*Thalysias*) *vulpina* (Lamarck, 1814)
Subfamily Ophilitaspongiinae de Laubenfels, 1936
Genus *Antho* Gray, 1867
Antho (*Acarnia*) *coriacea* (Bowerbank, 1874)
Antho (*Acarnia*) *spinulosa* (Tanita, 1968)
Genus *Echinoclathria* Carter, 1885
Echinoclathria arborea (Tanita, 1968)
Echinoclathria noto (Tanita, 1963)
Family Mycalidae Lundbeck, 1905
Genus *Mycale* Gray, 1867
Mycale (*Aegogropila*) *adhaerens* (Lambe, 1893)
Mycale (*Aegogropila*) *contarenii* (Lieberkühn, 1859)
Mycale (*Aegogropila*) *magellanica* (Ridley, 1881)
Mycale (*Aegogropila*) *parvasigma* Hoshino, 1981
Mycale (*Aegogropila*) *plumosa* sensu Hoshino, 1981
Mycale (*Carmia*) *nullarosette* Hoshino, 1981
Mycale (*Carmia*) *tenuisinuousitylostyli* Hoshino, 1981
Mycale (*Mycale*) *grandis* Gray, 1867
Mycale (*Mycale*) *lingua* (Bowerbank, 1866)
Mycale (*Mycale*) *macginitiei* de Laubenfels, 1930
Mycale (*Mycale*) *tylota* Koltun, 1958
Mycale (*Paresperella*) *macrosigma* (Lindgren, 1897)
Mycale (*Paresperella*) *undulata* Tanita, 1968
Mycale izuensis Tanita & Hoshino, 1989
Family Myxillidae Dendy, 1922
Genus *Myxilla* Schmidt, 1862
Myxilla (*Ectyomyxilla*) *parasitica* Lambe, 1893

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Myxilla (*Myxilla*) *behringensis* Lambe, 1895
Myxilla (*Myxilla*) *bivalvia* Tanita, 1967
Myxilla (*Myxilla*) *hiradoensis* Hoshino, 1981
Myxilla (*Myxilla*) *incrustans* (Johnston, 1842)
Myxilla (*Myxilla*) *incrustans cylindrica* Tanita & Hoshino, 1989
Myxilla (*Myxilla*) *lobata* Hoshino, 1981
Myxilla (*Myxilla*) *productus* Hoshino, 1981
Myxilla (*Myxilla*) *rosacea* (Lieberkühn, 1859)
Myxilla (*Myxilla*) *rosacea* var. *japonica* Ridley & Dendy, 1887
Myxilla (*Myxilla*) *setoensis* Tanita, 1961
Family Tedaniidae Ridley & Dendy, 1886
Genus *Tedania* Gray, 1867
Tedania (*Tedania*) *anhelans* (Vio in Olivi, 1792)
Tedania (*Tedania*) *brevispiculata* Thiele, 1903
Tedania (*Tedania*) *fragilis* Lambe, 1895
Tedania (*Tedania*) *levigotylota* Hoshino, 1981
Tedania (*Tedania*) *palola* Hoshino, 1981
Order Clionaida Morrow & Cárdenas, 2015
Family Acanthochaetetidae Fischer, 1970
Genus *Acanthochaetetes* Fischer, 1970
Acanthochaetetes wellsi Hartman & Goreau, 1975
Family Clionaidae d’Orbigny, 1851
Genus *Cliona* Grant, 1826
Cliona argus Thiele, 1898
Cliona argus var. *laevicollis* Thiele, 1898
Cliona celata Grant, 1826
Cliona lobata Hancock, 1849
Cliona infrafoliata (Thiele, 1898)
Cliona raromicrosclera (Dickinson, 1945)
Cliona reticulata Ise & Fujita, 2005
Genus *Pione* Gray, 1867
Pione concharum (Thiele, 1898)
Pione vastifica (Hancock, 1849)
Genus *Spheciospongia* Marshall, 1892
Spheciospongia inconstans (Dendy, 1887)
Spheciospongia panis (Thiele, 1898)
Spheciospongia rotunda (Tanita & Hoshino, 1989)
Family Placospongiidae Gray, 1867
Genus *Placospongia* Gray, 1867
Placospongia anthosigma (Tanita & Hoshino, 1989)
Family Spirastrellidae Ridley & Dendy, 1886
Genus *Spirastrella* Schmidt, 1868
Spirastrella abata Tanita, 1961
Spirastrella coccinea (Duchassaing & Michelotti, 1864)

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Spirastrella insignis Thiele, 1898
Order Tethyida Morrow & Cárdenas, 2015
Family Tethyidae Gray, 1848
Genus *Tethya* Lamarck, 1815
Tethya aurantium (Pallas, 1766)
Tethya deformis Thiele, 1898
Tethya diploderma Schmidt, 1870
Tethya japonica Sollas, 1888
Order Suberitida Chombard & Boury-Esnault, 1999
Family Halichondriidae Gray, 1867
Genus *Axinyssa* Lendenfeld, 1897
Axinyssa aculeata Wilson, 1925
Genus *Ciocalypta* Bowerbank, 1862
Ciocalypta expanda Tanita & Hoshino, 1989
Ciocalypta penicillus Bowerbank, 1862
Genus *Epipolasis* de Laubenfels, 1936
Epipolasis suluensis (Wilson, 1925)
Genus *Halichondria* Fleming, 1828
Halichondria (*Eumastia*) *sitiens* (Schmidt, 1870)
Halichondria (*Halichondria*) *cylindrata* Tanita & Hoshino, 1989
Halichondria (*Halichondria*) *japonica* (Kadota, 1922)
Halichondria (*Halichondria*) *okadai* (Kadota, 1922)
Halichondria (*Halichondria*) *oshoro* Tanita, 1961
Halichondria (*Halichondria*) *panicea* (Pallas, 1766)
Halichondria (*Halichondria*) *surrubicunda* Hoshino, 1981
Genus *Hymeniacidon* Bowerbank, 1858
Hymeniacidon flavia Sim & Lee, 2003
Hymeniacidon halichondroides (Thiele, 1898)
Hymeniacidon ovalae Tanita & Hoshino, 1989
Hymeniacidon perlevis (Montagu, 1814)
Hymeniacidon sphaerodigitata Bergquist, 1970
Genus *Topsentia* Berg, 1899
Topsentia disparilis (Lambe, 1893)
Topsentia fibrosa (Fristedt, 1887)
Topsentia kushimotoensis (Hoshino, 1977)
Topsentia rugosa (Ridley & Dendy, 1886)
Family Stylocordyidae Topsent, 1892
Genus *Stylocordyla* Thomson, 1873
Stylocordyla borealis (Lovén, 1868)
Stylocordyla longissima (Sars, 1872)
Family Suberitidae Schmidt, 1870
Genus *Aaptos* Gray, 1867
Aaptos aaptos (Schmidt, 1864)
Aaptos niger Hoshino, 1981

(continued)

Genus *Homaxinella* Topsent, 1916
Homaxinella brevistyla Hoshino, 1981
Homaxinella infundibula Tanita & Hoshino, 1989
Homaxinella ramosimassa Tanita & Hoshino, 1989
Homaxinella tanitai Hoshino, 1981
Genus *Pseudosuberites* Topsent, 1896
Pseudosuberites incrustans (Thiele, 1898)
Pseudosuberites kunisakiensis Hoshino, 1981
Pseudosuberites perforatus (Thiele, 1898)
Genus *Rhizaxinella* Keller, 1880
Rhizaxinella arborescens Thiele, 1898
Rhizaxinella burtoni Koltun, 1966
Rhizaxinella cervicornis Thiele, 1898
Rhizaxinella clavata Thiele, 1898
Rhizaxinella elevata Thiele, 1898
Rhizaxinella incrassata Thiele, 1898
Genus *Suberites* Nardo, 1833
Suberites aurantiacus (Duchassaing & Michelotti, 1864)
Suberites carnosus (Johnston, 1842)
Suberites domuncula (Olivi, 1792)
Suberites excellens (Thiele, 1898)
Suberites ficus (Johnston, 1842)
Suberites japonicus Thiele, 1898
Suberites placenta Thiele, 1898
Suberites sericeus Thiele, 1898
Suberites virgultosus (Johnston, 1842)
Genus *Terpios* Duchassaing & Michelotti, 1864
Terpios cf. *fugax* de Laubenfels, 1954
Terpios hoshinota Rützler & Muzik, 1993

References

Bavestrello G, Calcinai B, Cerrano C, Sara M (1998) *Alectona* species from north-western Pacific (Demospongiae: Clionidae). J Mar Biol Assoc UK 78:59–73

Bertolino M, Pica D, Bavestrello G, Iwasaki N, Calcinai B (2011) A new species of *Triptolemma* (Porifera: Pachastrellidae) from the Pacific Ocean with a revision of the genus. J Mar Biol Assoc UK 91:329–338

Burton M (1935) Some sponges from the Okhotsk Sea and the Sea of Japan. Issled Morei SSSR 22:64–81

Burton M (1963) A revision of the classification of the calcareous sponges: with a catalogue of the specimens in the British Museum (Natural History). Trustees of the British Museum (Natural History), London

Calcinai B, Azzini F, Bavestrello G, Iwasaki N, Cerrano C (2004) Redescription of *Alectona verticillata* (Johnson) (Porifera, Alectonidae) boring into Japanese precious coral. Ital J Zool 71:337–339

Calcinai B, Cerrano C, Iwasaki N, Bavestrello G (2008) Sponges boring into precious corals: an overview with description of a new species of *Alectona* (Demospongiae, Alectonidae) and a world-wide identification key for the genus. Mar Ecol 29:273–279

Cárdenas P, Pérez T, Boury-Esnault N (2012) Sponge systematics facing new challenges. Adv Mar Biol 61:79–209

Carter HJ (1885) Report on a collection of marine sponges from Japan, made by Dr. Anderson, F. R. S., Superintendent Indian Museum, Calcutta. Ann Mag Nat Hist 15:387–405

Döderlein L (1883) Studien an japanischen Lithistiden. Z Wiss Zool 40:62–104

Döderlein L (1892) No official title, an article by an anonymous contributor, providing Döderlein's description of *Petrostroma schulzei* n.g., n.sp. Verh Dtsch Zool Ges 2:143–145

Ereskovsky AV, Borchiellini C, Gazave E, Ivanisevic J, Lapebie P, Pérez T, Renard E, Vacelet J (2009) The homoscleromorph sponge *Oscarella lobularis*, a promising sponge model in evolutionary and developmental biology. Bioessays 31:89–97

Fujikura K, Lindsay D, Kitazato H, Nishida S, Shirayama Y (2010) Marine biodiversity in Japanese waters. PLoS ONE 5, e11836

Gravier MC (1899) Sur une collection d'eponges (hexactinellides) du Japon. Bull Mus Natl Hist Nat 5:419–423

Haeckel E (1872) Biologie der Kalkschwämme (Calcispongien oder Grantien). Georg Reimer, Berlin

Hara J (1894) On a new species of calcareous sponge, *Lelapia nipponica*. Zool Mag 6:369–370 [in Japanese]

Higa K, Fukuyama Y, Sekiya M, West RR, Nagai K, Sugiyama T (2010) Habitat of a living fossil, *Acanthochaetetes* (Class Demospongiae), along the Komesu Coast in the southern part of Okinawa Island. Sci Rep Fukuoka Univ 40:233–243 [in Japanese with English abstract]

Hirano K, Kubota T, Tsuda M, Watanabe K, Fromont J, Kobayashi J (2000) Ma'edamines A and B, cytotoxic bromotyrosine alkaloids with a unique 2(^{1}H)pyrazinone ring from sponge *Suberea* sp. Tetrahedron 56:8107–8110

Hooper JNA, Van Soest RWM (eds) (2002) Systema Porifera: a guide to the classification of sponges. Kluwer, New York

Hoshino T (1970) Mukaishima hukin (Stonaikai) yori erareta jinjōkaimen 15 shu. Bull Biol Soc Hiroshima Univ 36:21–26 [in Japanese]

Hoshino T (1971) Sponge fauna of Seto Inland Sea (Demospongiae, Calcarea). Bull Biol Soc Hiroshima Univ 38:21–30 [in Japanese]

Hoshino T (1974) Demospongiae of Hiryu-jima (Biro-jima), an islet in the Ariake Sea. Calanus 4:8–15 [in Japanese]

Hoshino T (1975a) The sponges of the Anan Coast. Zool Mag 84:30–38 [in Japanese]

Hoshino T (1975b) Some demosponges from oyster-rafts and oil-fences of Hiroshima Fisheries Experimental Station. Bull Biol Soc Hiroshima Univ 40:173–177 [in Japanese]

Hoshino T (1975c) Nine species of Demospongia from the coast of Hibiki-nada, Sea of Japan. Bull Biol Soc Hiroshima Univ 41:17–21

Hoshino T (1976a) Demosponges from the western coast of Kii Peninsula, Japan. Zool Mag 85:248–261

Hoshino T (1976b) *Axinella profunca* Ridley and Dendy (class Demospongia) from deep sea area off Kochi. Proc Jap Soc Syst Zool 12:1–4 [in Japanese]

Hoshino T (1976c) Demosponges obtained from the vicinity of the Aitsu Marine Biological Station. Calanus 5:3–11 [in Japanese]

Hoshino T (1976d) Number of Japanese demosponges. Zool Mag 85:506 [in Japanese]

Hoshino T (1977) Demosponges from the Kii Channel and its environs, western Japan. Proc Jap Soc Syst Zool 13:5–15

Hoshino T (1981a) Shallow-water demosponges of western Japan, I. J Sci Hiroshima Univ Ser B Div 1 Zool 29:47–205

Hoshino T (1981b) Shallow-water demosponges of western Japan, II. J Sci Hiroshima Univ Ser B Div 1 Zool 29:207–289

Hoshino T (1981c) Demosponges of Japanese waters and its vicinity. Circ Jap Soc Syst Zool 54:1–5 [in Japanese]

Hoshino T (1982) Description of the dominant species of the class Demospongia dredged from the coastal area of the Izu Peninsula, Sagami Bay. Mem Natl Sci Mus Tokyo 15:139–148

Hoshino T (1985a) *Dysidea minna* sp. nov., a new dysideid demosponge from the Ryukyus. Galaxea 4:49–52

Hoshino T (1985b) Description of two new species in the genus *Agelas* (Demospongia) from Zamami Island, the Ryukyus, Japan. Proc Jap Soc Syst Zool 30:1–10

Hoshino T (1985c) Five demosponges associated with molluscs. Spec Publ Mukaishima Mar Biol Stn 1985:135–138

Hoshino T (1986) Check list of the marine Demospongia (Porifera) from Japanese waters. Mukaishima Marine Biological Station Hiroshima, Onomichi

Hoshino T (1987a) A preliminary report on demosponges from the coral reef of the Okinawa Isldands. Galaxea 6:25–29

Hoshino T (1987b) Preliminary catalogue of the marine sponges of the class Demospongia (Porifera) from Japanese waters. Mukaishima Marine Biological Station Hiroshima, Onomichi

Hoshino T (1990) *Merlia tenuis* n. sp. encrusting shell surfaces of gastropods, *Chicoreus*, from Japan. In: Rützler K (ed) New perspectives in sponge biology. Smithsonian Institution Press, Washington, DC, pp 295–301

Hoshino S, Ise Y, Watanabe Y (2003) Phylum Porifera. In: Union of Japanese Societies for Systematic Biology (ed) Japanese biota species number survey, 1st edn. http://ujssb.org/biospnum/search.php

Hoshino S, Takeda M, Watanabe Y (2004) Systematic status of *Halichondria japonica* (Kadota) (Demospongiae, Halichondrida) from Japan. Boll Mus Inst Biol Univ Genova 68:373–379

Hoshino S, Saito SD, Fujita T (2008) Contrasting genetic structure of two *Hymeniacidon* species. Hydrobiologia 603:313–326

Hôzawa S (1916) On some Japanese calcareous sponges belonging to the family Heteropiidae. J Coll Sci Imp Univ Tokyo 38(Art 5):1–41

Hôzawa S (1918) Report on the calcareous sponges collected during 1906 by the United States Fisheries steamer *Albatross* in the northwestern Pacific. Proc US Natl Mus 54:525–556

Hôzawa S (1923) On a new genus of calcareous sponge. Annot Zool Jpn 10:183–190

Hôzawa S (1928) Report on the biological survey of Mutsu Bay. 6. Calcarea of Mutsu Bay. Sci Rep Tohoku Imp Univ Ser 4 3:119–221

Hôzawa S (1929) Studies on the calcareous sponges of Japan. J Fac Sci Imp Univ Tokyo 1:277–389

Hôzawa S (1933a) Nihon kankai no sekkai kaimen. Zool Mag 45:99–101 [in Japanese]

Hôzawa S (1933b) Sekkai kaimen toha nanika? Shokubutsu Doubutsu 1:163–170 [in Japanese]

Hôzawa S (1933c) Report on the calcareous sponges obtained by the survey of the continental shelf bordering on Japan. Sci Rep Tohoku Imp Univ Ser 4(8):1–20

Hôzawa S (1940a) On some calcareous sponges from Japan. Sci Rep Tohoku Imp Univ 15:29–58

Hôzawa S (1940b) Report on the calcareous sponges obtained by the Zoological Institute and Museum of Hamburg. Sci Rep Tohoku Imp Univ 15:131–163

Hôzawa S (1940c) Class Calcarea (Phylum Porifera). Fauna Nipponica 2:1–88 [in Japanese]

Hôzawa S, Tanita S (1941) The fauna of Akkeshi Bay. XII. Calcarea. J Fac Sci Hokkaido Imp Univ Ser VI Zool 7:421–429

Hôzawa S, Tanita S (1965) Calcarea (Porifera). In: Okada Y, Uchida S, Uchida T (eds) New illustrated encyclopedia of the fauna of Japan, vol 1. Hokuryūkan, Tokyo, pp 141–146 [in Japanese]

Ijima I (1894) Notice of new Hexactinellida from Sagami Bay. I. Zool Anz 17:365–369

Ijima I (1895) On two new Hexactinellida from Sagami Bay. Zool Mag 7:93–96

Ijima I (1896) Notice of new Hexactinellida from Sagami Bay. Zool Anz 19:249–254

Ijima I (1897) Revision of hexactinellids with discotasters, with descriptions of five new species. Annot Zool Jpn 1:43–59

Ijima I (1898) The genera and species of Rossellidae. Annot Zool Jpn 2:41–55

Ijima I (1901) Studies on the Hexactinellida contribution I. (Euplectellidae). J Coll Imp Univ Tokyo 15(part I):1–299

Ijima I (1902a) Note on *Walteria leuckalti* Ij. Annot Zool Jpn 4:119–122

Ijima I (1902b) Studies on the Hexactinellida Contribution II. (The genera *Corbitella* and *Heterotella*). J Coll Imp Univ Tokyo 17(Art 9):1–34

Ijima I (1902c) Ueber die von mir in der Sagami-See gesammelten Hexactinelliden. In: Matschie P (ed) Verhandlungen des V. Internationalen Zoologen-Congresses zu Berlin, 12–16. August 1901. Gustav Fischer, Jena, pp 689–692

Ijima I (1903) Studies on the Hexactinellida. Contribution III. Placosoma, a new Euplectellid; Leucopsacidae and Caulophacidae. J Coll Imp Univ Tokyo 18(Art 1):1–124

Ijima I (1904) Studies on the Hexactinellida. Contribution IV. Rossellidae. J Coll Imp Univ Tokyo 19(Art 7):1–307

Ijima I (1916) Notes on *Aphrocallistes beatrix* Gray, particularly with reference to the form occurring in East Asiatic seas. Annot Zool Jpn 9:173–183

Ijima I (1927) The Hexactinellida of the *Siboga* Expedition. Siboga Expeditie 6:1–383

Ijima I, Okada Y (1938) Studies on the Hexactinellida. Contribution V. (Pheronematidae and Hyalonematidae). J Coll Sci Imp Univ Tokyo 4:413–469

Ise Y (2013) From taxonomy to zoology–case study of sponge, "a fourth class of phylum Porifera: Homoscleromorpha". Taxa Proc Jap Soc Syst Zool 34:18–24 [in Japanese with English abstract]

Ise Y, Fujita T (2005) A new boring sponge of the genus *Cliona* (Demospongiae: Clionaidae) from the Ryukyu Islands, southwestern Japan. Species Divers 10:37–43

Ise Y, Vacelet J (2010) New carnivorous sponges of the genus *Abyssocladia* (Demospongiae, Poecilosclerida, Cladorhizidae) from Myojin Knoll, Izu-Ogasawara Arc, southern Japan. Zool Sci 27:888–894

Ise Y, Takeda M, Watanabe Y (2004) Psammobiontic Clionaidae (Demospongiae: Hadromerida) in lagoon of the Ryukyu Islands, southwestern Japan. Boll Mus Inst Biol Univ Genova 68:381–389

Kadota J (1922) Tanjiku kaimen *Reniera* zoku nishinshu no shokansatsu. Zool Mag (Tokyo) 34:700–711 [in Japanese]

Kita M, Gise B, Kawamura A, Kigoshi H (2003) Stylissatin A, a cyclic peptide that inhibits nitric oxide production from the marine sponge *Stylissa massa*. Tetrahedron Lett 54:6826–6828

Koltun VM (1958) Cornacuspongia of sea waters washing the South Sakhalin and the South Kurile Island region. Issled Dal'nevost Mor SSSR 5:42–77 [in Russian]

Koltun VM (1959) [Siliceous horny sponges of the northern and fareastern seas of the U.S.S.R.] Opredeliteli po faune SSR, izdavaemye Zoologicheskim muzeem. Akademii Nauk 67:1–236 [in Russian]

Koltun VM (1962) Four rayed and siliceous horny sponges from the Pacific shallow waters of Paramushir and Shumshu Islands. Issled Dal'nevost Mor SSSR 8:181–199 [in Russian]

Koltun VM (1966) [Four rayed sponges of northern and far eastern sea of the USSR.] Opredeliteli po faune SSR, izdavaemye Zoologicheskim muzeem Akademii Nauk 94:1–124 [in Russian]

Kyodo N (1934) Brief history of studies of Japanese freshwater sponges. Zool Mag (Tokyo) 46:280–286 [in Japanese]

Lampe W (1886) *Tetilla japonica*, eine neue Tetractinellidenform mit radiärem Bau. Arch Nat 52:1–18

Lebwohl F (1914a) Japanische Tetraxonida, I. *Sigmatophora* und II. *Astrophora metastrosa*. J Coll Sci Imp Univ Tokyo 35(2):1–116

Lebwohl F (1914b) Japanische Tetraxonida. III. *Euastrosa* und IV. *Sterrastrosa*. J Coll Sci Imp Univ Tokyo 35(5):1–70

Lévi C (1953) Description de *Plakortis nigra* nov. sp. et remarques sur les Plakinidae (Démosponges). Bull Mus Natl Hist Nat 25:320–328

Lindgren NG (1897) Beitrag zur Kenntnis der Spongienfauna des malaiischen Archipels und der chinesischen Meere. Zool Anz 20:480–487

Lindgren NG (1898) Beitrag zur Kenntniss der spongienfauna des malayischen Archipels und der chinesischen Meere. Zool Jb Abt Syst Geogr Biol Thiere 11:283–378

Maldonado M (2002) Family Pachastrellidae Carter, 1875. In: Hooper JNA, Van Soest RWM (eds) Systema Porifera: a guide to the classification of sponges. Kluwer, New York, pp 141–162

Masuda Y (2006) An overview of Japanese freshwater sponges. Taxa Proc Jap Soc Syst Zool 20:15–22 [in Japanese with English abstract]

Mizoguchi H (1998) The sponge in the history of Japanese biology. In: Watanabe Y, Fusetani N (eds) Sponge sciences: multidisciplinary perspectives. Springer, Tokyo, pp 427–439

Morrow C, Cárdenas P (2015) Proposal for a revised classification of the Demospongiae (Porifera). Front Zool 12:7

Muricy G (2011) Diversity of Indo-Australian *Plakortis* (Demospongiae: Plakinidae), with description of four new species. J Mar Biol Assoc UK 91:303–319

Muricy G, Diaz MC (2002) Order Homosclerophorida Dendy, 1905, Family Plakinidae Schulze, 1880. In: Hooper JNA, Van Soest RWM (eds) Systema Porifera: a guide to the classification of sponges. Kluwer, New York, pp 71–82

Nakagawa H (1897) Report on simple calcareous sponge *Sycandra*. Zool Mag 9:341–346 [in Japanese]

Ogawa K (1997) A nominal list of Porifera reported from Japan. I. Class Hexactinellida. Nankiseibutu 39:67–70 [in Japanese]

Ogawa K (1999) A nominal list of Porifera reported from Japan. II. Class Calcarea. Nankiseibutu 41:67–73 [in Japanese]

Ogawa K (2001) A nominal list of Porifera reported from Japan. III. Class Demospongia (1). Nankiseibutu 43:63–71 [in Japanese]

Ogawa K (2002) A nominal list of Porifera reported from Japan. III. Class Demospongia (2). Nankiseibutu 44:157–166 [in Japanese]

Ogawa K (2003) A nominal list of Porifera reported from Japan. III. Class Demospongia (3). Nankiseibutu 45:120–124 [in Japanese]

Ogawa K (2004) Revised nominal list of Demospongiae reported from Japan. Nankiseibutu 46:154–158 [in Japanese]

Ogawa K (2006) Porifera of the Sagami Sea. Mem Natl Sci Mus Tokyo 40:23–56

Ogawa K (2010) Notes on Japanese Demospongiae: 2. Hermit-crab inhabiting sponges of the genus *Suberites* (Hadromerida, Suberitidae) in Japan. Bull Biogeogr Soc Jpn 65:81–89 [in Japanese]

Ogawa K, Ito K (2008) Notes on Japanese Demospongiae: 1. New distributional records of the genus *Agelas* (Agelasida, Agelasidae). Bull Biogeogr Soc Jpn 63:63–70 [in Japanese]

Ogawa K, Yokochi H, Matsuzaki K (1993) Taxonomical and ecological notes on the sclerosponges newly found at Amitori Bay, Iriomote Island, Okinawa, Japan. Nankiseibutu 35:33–38 [in Japanese]

Ogawa K, Abe W, Ueshima R (2012) Report on the poriferan specimens deposited in the Department of Zoology, the University Museum, the University of Tokyo. (1) Hexactinellida. The University Museum, the University of Tokyo, Tokyo

Okada Y (1925) On an interesting hexactinellid, *Calyptorete ijimai* nov. gen. et nov. sp. Ann Zool Jpn 10:285–298

Okada (1928) On the development of a hexactinellid sponge, *Farrea sollasii*. Tokyo Univ J Fac Sci Sec 4 Zool 2:1–27

Okada Y (1932) Report on the hexactinellid sponges collected by the United States fisheries steamer *Albatoross* in the northwestern Pacific during the summer of 1906. Proc US Natl Mus 81:1–118

Okada Y (1937) Ijima Isao sensei no koto domo. Kagaku-chisiki 17:82–84 [in Japanese]

Otani M (2012) Morphological description of *Hymeniacidon flavia* Sim and Lee, 2003 Demospongiae, (Halichondriidae) from Osaka Bay, Japan and a proposal for the new Japanese name of Kiiro-isokaimen. Bull Osaka Mus Nat His 66:1–7 [in Japanese with English abstract]

Pisera A, Lévi C (2002) Family Vetulinidae Lendenfeld, 1903. In: Hooper JNA, Van Soest RWM (eds) Systema Porifera: a guide to the classification of sponges. Kluwer, New York, pp 363–365

Poléjaeff N (1884) Report on the Keratosa collected by H.M.S. 'Challenger' during the years 1873–1876. Rep Sci Challenger Zool 11:1–88

Reiswig HM (1990) Correction of Ijima's (1927) list of recent Hexactinellid sponges (Porifera). Proc Biol Soc Wash 103:731–745

Rho BJ, Sim CJ (1976) On the classification and the distribution of the marine benthic animals in Korea, 4. Sponges. J Korean Res Inst Bet Liv Ewha Womans Univ 16:67–87

Rho BJ, Sim CJ (1979a) Three new species of Tetractinomorpha (Choristida, Hadromerida and Axinellida) from Jeju Islands in Korea. Korean J Zool 22:125–133

Rho BJ, Sim CJ (1979b) A taxonomic study on the Korean Sponges. 1. Poecilosclerida. J Korean Res Inst Bet Liv Ewha Womans Univ 23:61–67

Rho BJ, Sim CJ (1979c) Comparative morphology on parent and embryo of *Tetilla austral* in Korea. J Korean Res Inst Bet Liv Ewha Womans Univ 24:25–30

Rho BJ, Sim CJ (1981a) A taxonomic study on the marine sponges in Korea. 3. Choristida. J Korean Res Inst Bet Liv Ewha Womans Univ 28:55–65

Rho BJ, Sim CJ (1981b) One new species of Tetractinomorpha (Spirophorida) from Chugsan in Korea. Korean J Zool 24:145–150

Ridley SO, Dendy A (1887) Report on the Monaxonida collected by H.M.S. 'Challenger' during the years 1873–1876. Rep Sci Challenger Zool 20(59):1–275

Row RWH, Hôzawa S (1931) Report on the Calcarea obtained by the Hamburg South-West Australian Expedition of 1905. Sci Rep Tohoku Imp Univ 6:727–809

Schulze FE (1886) Über den Bau und das System der Hexactinelliden. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin (Physikalisch-Mathematisch Classe) 1886:1–97

Schulze FE (1887) Report on the Hexactinellida collected by H.M.S 'Challenger' during the years 1873–1876. Rep Sci Challenger Zool 21:1–514

Sim CJ (1981a) A systematic study on the marine sponges in Korea. 1. Ceractinomorpha and Tetractinomorpha. Soongjun Univ Essay Paper 11:83–105

Sim CJ (1981b) A taxonomic study on the marine sponges in Korea. 2. Hadromerida. Korean J Zool 24:9–17

Sollas WJ (1888) Report on the Tetractinellida collected by H.M.S. Challenger, during the years 1873–1876. Rep Sci Challenger Zool 25(63):1–458

Tanita S (1939) Two new Calcarea obtained from Saseho, Japan. Sci Rep Tohoku Imp Univ 14:319–326

Tanita S (1940) Calcareous sponges of Matsushima Bay. Sci Rep Tohoku Imp Univ 15:165–177

Tanita S (1941a) Report on the biological survey of Mutsu Bay. 35. Studies on the Calcarea of Mutsu Bay. Sci Rep Tohoku Imp Univ 16:1–7

Tanita S (1941b) Calcareous sponges obtained from Onagawa Bay and its vicinity. Sci Rep Tohoku Imp Univ 16:263–282

Tanita S (1942a) Calcareous sponges collected in the Kanto district, Japan. Sci Rep Tohoku Imp Univ 17:17–69

Tanita S (1942b) Key to all the described species of the genus *Leucosolenia* and their distribution. Sci Rep Tohoku Imp Univ 17:71–93

Tanita S (1942c) Report on the calcareous sponges obtained by the Zoological Institute and Museum of Hamburg. Part II. Sci Rep Tohoku Imp Univ 17:105–135

Tanita S (1943) Studies on the Calcarea of Japan. Sci Rep Tohoku Imp Univ 17:353–490

Tanita S (1948) Hokkaido no sekkai kaimen (yohou). Zool Mag 58:86–87 [in Japanese]

Tanita S (1958) Sponges collected from oyster-rafts in Matsushima Bay and its adjacent waters. Bull Tohoku Reg Fish Res Lab 11:127–143

Tanita S (1961a) Two sponges obtained by the training ship "Oshoro maru" in the eastern Berling Sea. Bull Fac Fish Hokkaido Univ 11:183–187

Tanita S (1961b) Report on the sponges collected from the Kurushima Strait, Seto Inland Sea. Mem Ehime Univ Sect II (B) 4:335–354

Tanita S (1961c) Report on the non-calcareous sponges in the Museum of the Biological Institute of the Tohoku University. Part I. Sci Rep Tohoku Univ Ser 4 Biol 27:131–140

Tanita S (1963) Report on the non-calcareous sponges in the Museum of the Biological Institute of the Tohoku University. Part II. Sci Rep Tohoku Univ Ser 4 Biol 29:121–129

Tanita S (1964) Noto Tsukumo wan engan no kaimen. Annu Rep Noto Mar Biol Lab 4:15–22 [in Japanese]

Tanita S (1965a) Report on the sponges obtained from the adjacent waters of the Sado Island, Japan Sea. Bull Jap Sea Reg Fish Res Lab 14:43–66

Tanita S (1965b) Two sponges from the southeastern region of the Japan Sea. Bull Jap Sea Reg Fish Res Lab 14:67–70

Tanita S (1965c) Demospongiae (Porifera). In: Okada Y, Uchida S, Uchida T (eds) New illustrated encyclopedia of the fauna of Japan, vol 1. Hokuryūkan, Tokyo, pp 154–163 [in Japanese]

Tanita S (1967) Report on the sponges obtained from Tajima District, southwestern region of the Japan Sea. Bull Jap Sea Reg Fish Res Lab 17:111–126

Tanita S (1968) Sponge-fauna of the Ariake Sea. Bull Seikai Reg Fish Res Lab 36:39–63

Tanita S (1969) Further studies on the sponges obtained from the Sado Island and its adjacent waters. Bull Jap Sea Reg Fish Res Lab 21:67–88

Tanita S (1970a) Sponge-fauna of Sagami Bay, especially the Demospongiae. Bull Tohoku Reg Fish Res Lab 30:87–97 [in Japanese with English abstract]

Tanita S (1970b) The sponges in the Tokushima Museum. Bull Tohoku Reg Fish Res Lab 30:99–105 [in Japanese]

Tanita S (1977) Sponges obtained from Kii-Shirahama and its vicinity. Publ Seto Mar Biol Lab 24:29–41

Tanita S (1978) Sponges obtained by trawl net from the Sado Strait. Bull Jap Sea Reg Fish Res Lab 29:229–237

Tanita S, Hoshino T (1989) The Demospongiae of Sagami Bay. Biological Laboratory, Imperial Household, Tokyo

Thiele J (1898) Studien über pazifische Spongien. I. Japanische Demospongien. Zoologica. Original-Abhandlungen aus dem Gesamtgebiete der Zoologie Stuttgart 24:1–72

Topsent E (1928a) Sur deux eurétides du Japon (note préliminaire). Bull Inst Oceanogr 515:1–4

Topsent E (1928b) Éponges des côtes du Japon. Collection du Musée Océanographique de Monaco. Ann Inst Oceanogr 6:297–319

Topsent E (1930) *Chondrocladia yatsui* n. sp., de la Baie de Sagami. Ann Zool Jpn 12:421–432

Tsuda M, Sakuma Y, Kobayashi J (2001) Suberedamines A and B, new bromotyrosine alkaloids from a sponge *Suberea* species. J Nat Prod 64:980–982

Vacelet J (2002) Recent 'Sphinctozoa,' Order Verticillitida, Family Verticillitidae Schramann, 1882. In: Hooper JNA, Van Soest RWM (eds) Systema Porifera: a guide to the classification of sponges. Kluwer, New York, pp 1097–1098

Vacelet J, Borojevic R, Boury-Esnault N, Manuel M (2002) Order Lithonida Vacelet, 1981, recent. In: Hooper JNA, Van Soest RWM (eds) Systema Porifera: a guide to the classification of sponges. Kluwer, New York, pp 1185–1192

Van Soest RWM, Beglinger EJ, Vooged NJD (2010) Skeletons in confusion: a review of astrophorid sponges with (dicho-)calthrops as structural megascleres (Porifera, Demospongiae, Astrophorida). ZooKeys 68:1–88

Van Soest RWM, Boury-Esnault N, Hooper JNA, Rützler K, Voogd NJd, Alvarez de Glasby B, Hajdu E, Pisera A, Manconi R, Schönberg C, Janussen D, Tabachnick KR, Klautau M, Picton B, Kelly M, Vacelet J, Dohrmann M, Díaz M-C, Cárdenas P (2015a) World Porifera database. Accessed at http://www.marinespecies.org/porifera on 16 Dec 2015

Van Soest RWM, Hoeksema BW, Reimer JD, Vooged NJD (2015b) New records of the rare calcareous sponge *Paragrantia waguensis* Hôzawa, 1940. Zookeys 546:1–20

Wörheide G (2008) A hypercalcified sponge with soft relatives: *Vaceletia* is a keratose demosponge. Mol Phylogenet Evol 47:433–438

Yamaguchi M, Miyazaki M, Kodrasov MP, Rotinsulu H, Losung F, Mangindaan REP (2003) Spongiacidin C, a pyrrole alkaloid from the marine sponge *Stylissa massa*, functions as a USP7 inhibitor. Bioorg Med Chem Lett 23:3884–3886

Chapter 14

Zoantharia (Cnidaria: Anthozoa: Hexacorallia) Diversity Research in Japan: Current State and Future Trends

James Davis Reimer and Takuma Fujii

Abstract The order Zoantharia (Cnidaria: Hexacorallia) comprises benthic anthozoans found in most of the world's marine ecosystems. Although historically understudied, research during the past 20 years has helped clarify our understanding of the diversity of this group. Much of this research on this group has originated from Japanese waters and has shown higher-level taxa (above genus) zoantharian diversity here to be among the highest recorded of any region in the world. Here, we introduce the overall species and higher-level zoantharian diversity as it is currently understood in Japan, and focus particularly on taxa that have been described or recorded from this country. Within Japan, taxonomic, phylogenetic, and ecological research has primarily focused on the southwestern Pacific Coast and the Ryukyu Archipelago, with little to no research performed in the Sea of Japan or in northern Japan. Additionally, results suggest that the deep sea, as well as other under-examined ecosystems such as rubble and muddy areas, still harbors much unknown zoantharian diversity. Even from relatively well-researched areas such as the Ryukyu Islands, data indicate that there are still many undescribed species. In the near future, more basic research efforts are needed before we can accurately estimate the diversity of Zoantharia. The methods and analyses used in recent studies of Japanese Zoantharia, as well as the new ideas proposed here, can be utilized in the near future in Japan and other marine regions to help us obtain a broader, more global understanding of zoantharian species distribution, biogeography, and diversity.

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14.1 Introduction

The order Zoantharia Gray, 1832 is a member of the class Anthozoa and the subclass Hexacorallia, most closely related to the sea anemones (order Actiniaria) (Fujii and Reimer 2013). In overall gross morphology, zoantharians resemble the actiniarians to some degree, and hence their common names, 'colonial sea anemones' and 'encrusting sea anemones.' Similar to actiniarians, zoantharians are soft bodied (with some exceptions), with an oral disk surrounded by tentacles; these tentacles retract and the oral disk 'closes' when disturbed or bringing food to the mouth (oral opening). However, there are some important and clear differences between zoantharians and actiniarians. Zoantharians are amazingly uniform in their polyp morphology, with all species having two rows of tentacles around the outside of their oral disk (Figs. 14.1 and 14.2), in contrast to actiniarians, which have much more variety in their tentacle arrangements. Nematocysts (cnidae, stinging cells) are smaller and simpler than those of many sea anemones, with only seven nematocyst types reported from zoantharians (Ryland and Lancaster 2004). Additionally, as their common name indicates, most species (but not all) are colonial, with polyps connected by a common tissue, or coenenchyme. The coenenchyme may be well developed, as in some *Palythoa* spp. (Fig. 14.1h), or a simple stolon between polyps, as in *Umimayanthus* sp. (Fig. 14.1m).

Within Zoantharia there are two major suborders; Macrocnemina Haddon and Shackleton, 1891, and Brachycnemina Haddon and Shackleton, 1891. Although recent research based on molecular phylogenetics has shown that Macrocnemina is polyphyletic (Sinniger et al. 2005), for practical purposes as well as ecological similarities, these two large suborders are a useful way to divide Zoantharia.

Macrocnemina contains families, genera, and species found from shallow coral reefs and rocky shorelines to the deep sea, and includes many epibiotic species that are commensal upon other organisms. Species of Macrocnemina can be differentiated by the fifth mesentery from the dorsal directive always being complete, as opposed to those in Brachycnemina in which the fifth mesentery is always incomplete (Fig. 14.2). Most members of Macrocnemina are planktonivores or detritivores, with food items obtained via their tentacles from the water column. It appears that the epibiotic behavior of many species is a method to reach further into the water column, or to be attached/associated with other animals that can provide detritus for them. Species of Macrocnemina are known to associate with mollusks, crustaceans, eunicid polychaetes, hydroids, sponges, black corals (Antipatharia), and octocorals. Recent studies have clearly pointed to the phylogenetic importance of these associations (Sinniger et al. 2005).

Most (but not all; see Irei et al. 2015) of the species within Brachycnemina are zooxanthellate, containing endosymbiotic dinoflagellates, *Symbiodinium* spp. Thus,

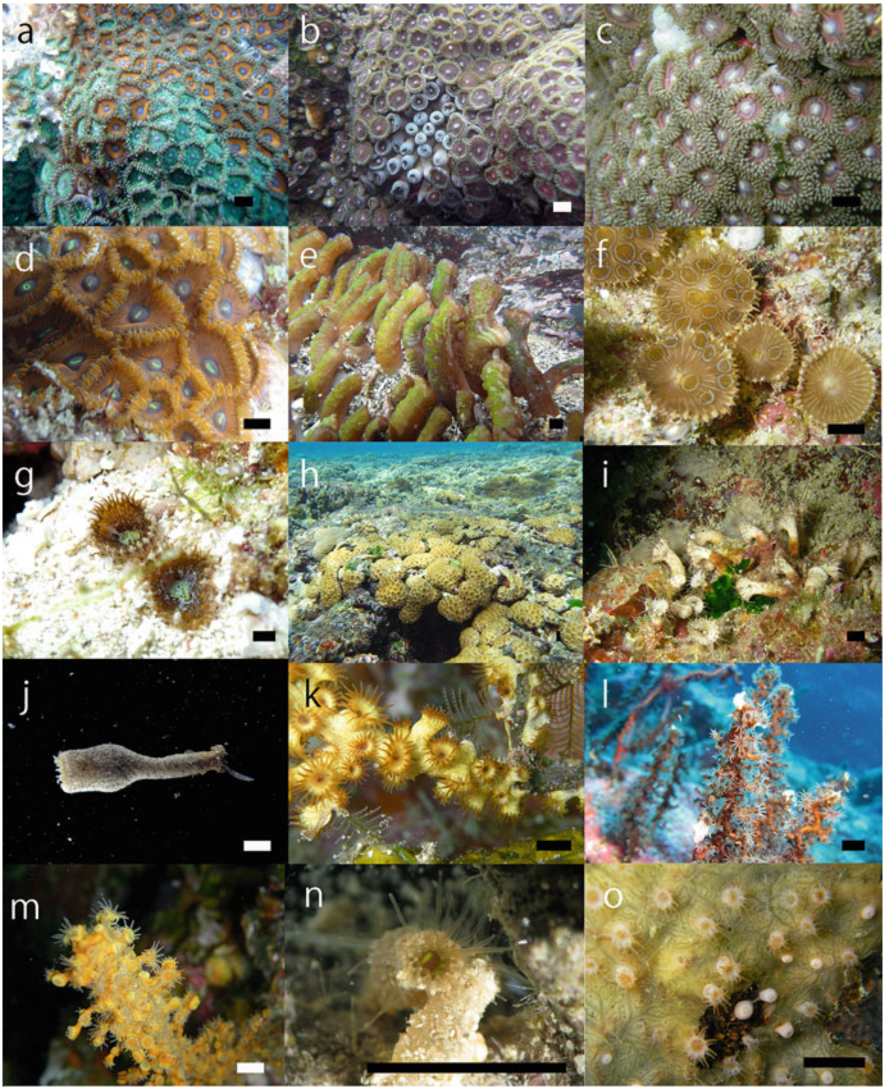

Fig. 14.1 Some common zoantharian species in Japanese waters. (**a**) *Zoanthus sansibaricus* Carlgren, 1900. (**b**) *Zoanthus* aff. *vietnamensis* Pax and Müller, 1957, (**c**) *Z. kuroshio* Reimer and Ono, 2006 in Reimer et al., 2006, (**d**) *Z. gigantus* Reimer and Tsukahara, 2006 in Reimer et al., 2006, (**e**) *Isaurus tuberculatus* Gray, 1828, (**f**) *Palythoa heliodiscus* (Ryland and Lancaster, 2003), (**g**) *P. mutuki* (Haddon and Shackleton, 1891), (**h**) *P. tuberculosa* (Esper, 1805), (**i**) *P. mizigama* Irei et al., 2015, (**j**) *Sphenopus exilis* Fujii and Reimer, 2016, (**k**) *Hydrozoanthus gracilis* (Lwowsky, 1913), (**l**) *Epizoanthus inazuma* Kise and Reier, 2016, (**m**) *E. illoricatus* Tischbierek, 1930, (**n**) *Microzoanthus occultus* Fujii and Reimer, 2013, (**o**) *Umimayanthus champuru* Montenegro et al., 2015. Scale bars approximately 10 mm

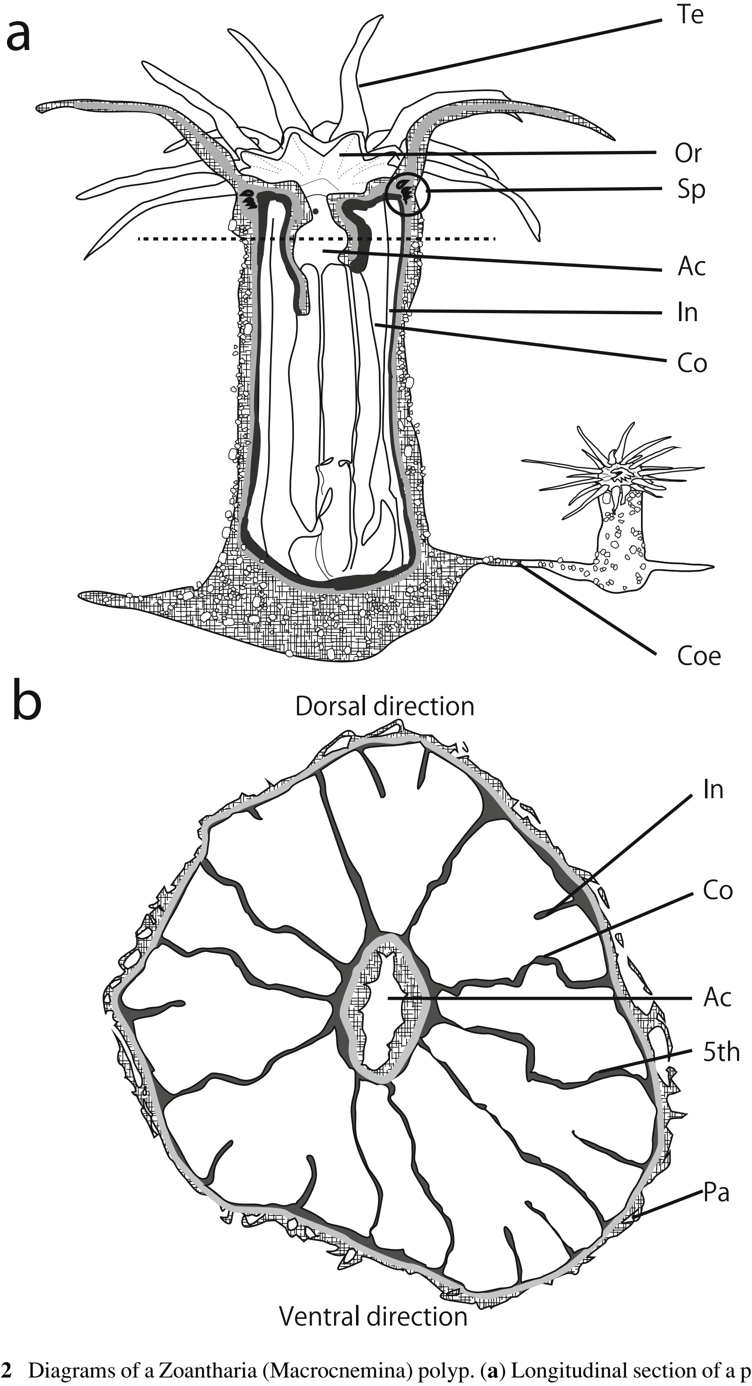

Fig. 14.2 Diagrams of a Zoantharia (Macrocnemina) polyp. (**a**) Longitudinal section of a polyp of *Microzoanthus kagerou* Fujii and Reimer, 2013. (**b**) Cross (*horizontal*) section of a polyp of *M*. *kagerou*. The ectoderm layer is shown in *mesh* pattern, mesoglea in *gray*, and endoderm in *black*. *Ac* actinopharynx, *Co* complete mesentery, *Coe* coenenchyme, *In* incomplete mesentery, *Or*

as a consequence, most species in this group are limited to shallow tropical or subtropical regions, and in Japan primarily within the region influenced by the warm Kuroshio Current (Fig. 14.3). In particular, species of the genera *Zoanthus* Lamarck, 1801 (Zoanthidae) and *Palythoa* Lamouroux, 1816 (Sphenopidae) are commonly seen even in intertidal coral reef flats, and, compared to most macrocneminans, have been well studied both in Japan and overseas.

Finally, there are some zoantharian species that are currently not within either suborder (*incertae sedis*), belonging to the deep-sea family Abyssoanthidae and genus *Abyssoanthus* (both Reimer and Fujiwara in Reimer et al. 2007a). Other recently described groups such as Microzoanthidae and Nanozoanthidae, although currently within the Macrocnemina, are phylogenetically distinct from other zoantharians; clearly, higher-level suborder reorganization is needed (Fujii and Reimer 2013).

The history of research on the systematics and diversity of Zoantharia stretches back to almost the beginning of binomial zoological nomenclature (e.g., *Zoanthus sociatus* (Ellis, 1768)), with most early taxonomic work being performed from specimens from the waters of Europe and the Caribbean, as is commonly seen in many other marine organisms. As with other taxa, as new discoveries and reexaminations came to light, our understanding of Zoantharia has changed with time. Zoantharian research in Japan dates back to the beginning of the last century with works by Lwowsky (1913), Tischbierek (1929), and Carlgren (1934) describing Macrocnemina species from the mainland of Japan. However, aside from some guidebooks (e.g., Uchida and Soyama 2001), little remained known about zoantharian diversity in Japanese waters until the past 15 years.

In recent years, there has been a large increase in the research conducted on Zoantharia in Japan, and specimens from Japanese waters have had key roles in the revision and reformation of the entire Zoantharia order (Tables 14.1 and 14.2). For example, during the past decade, Macrocnemina has undergone a dramatic taxonomic revision based on a reassessment of substrate specificity combined with the results of molecular phylogenetic analyses (Sinniger et al. 2005, 2010). For example, of the 20 genera currently placed within Macrocnemina, 13 have been erected since 2008 (Table 14.1). Taxa described from Japan include the genera *Umimayanthus* Montenegro et al., 2015, *Corallizoanthus* Reimer in Reimer et al., 2008, and the families Nanozoanthidae Fujii and Reimer, 2013 and Microzoanthidae Fujii and Reimer, 2011. As well, unusual species such as the azooxanthellate *Palythoa umbrosa* Irei et al., 2015 and *P. mizigama* Irei et al., 2015 have recently been described from Japan (Table 14.2).

The result of this recent research from Japanese waters is that, currently, Japan may be the most diverse location in the world in terms of Zoantharia. However, much of this may be the result of sampling bias, as the Coral Triangle region, noted

Fig. 14.2 (continued) oral disc, *Sp* sphincter muscle, *Te* tentacle, *5th* 5th dorsal mesentery. Note that in Brachycnemina the fifth mesentery from the dorsal directive would be incomplete, not complete

Table 14.1 Order Zoantharia taxonomy (genus level and higher) with number of genera, species recorded from Japan, and species described from Japan; taxa in *bold* described from Japan

Suborder	Family	Genus	Type species	A	B	C
Brachycnemina	Zoanthidae	*Zoanthus* Lamarck, 1801	*Zoanthus sociatus* (Lamarck, 1801)	23	4	2
		Isaurus Gray, 1828	*Isaurus tuberculatus* Gray, 1828	3	1	0
		Acrozoanthus Saville-Kent, 1893	*Acrozoanthus australiae* Saville-Kent, 1893	1	0	0
	Sphenopidae	*Palythoa* Lamouroux, 1816	*Palythoa mammillosa* (Ellis and Solander, 1786)	96	5	2
		Sphenopus Steenstrup, 1856	*Sphenopus marsupialis* (Gmelin, 1791)	4	2	1
	Neozoanthidae	*Neozoanthus* Herberts, 1972	*Neozoanthus tulearensis* Herberts, 1972	3	1	1
Macrocnemina	Epizoanthidae	*Epizoanthus* Gray, 1867	*Epizoanthus papillosus* Johnston, 1842	87	5	4
		Paleozoanthus Carlgren, 1924	*Paleozoanthus reticulatus* Carlgren, 1924	1	0	0
		Thoracatis Gravier, 1918	*Thoracactis topsenti* Gravier, 1918	1	0	0
	Hydrozoanthidae	*Hydrozoanthus* Sinniger et al., 2010	*Hydrozoanthus tunicans* (Duerden, 1900)	3	1	1
		Terrazoanthus Reimer and Fujii, 2010	*Terrazoanthus onoi* Reimer and Fujii, 2010	2	0^{a}	0
	Parazoanthidae	*Savalia* Nardo, 1844	*Savalia savaglia* (Bertoloni, 1819)	2	0	0
		Bergia Duchassaing de Fonbressin and Michelotti, 1860	*Bergia catenularis* Duchassaing de Fonbressin and Michelotti, 1860	3	0	0
		Parazoanthus Haddon and Shackleton, 1891	*Parazoanthus axinellae* Schmidt, 1862	13	0^{a}	0
		Isozoanthus Carlgren in Chun, 1903	*Isozoanthus giganteus* Carlgren in Chun, 1903	17	0	0
		Corallizoanthus Reimer in Reimer Nonaka Sinniger and Iwase, 2008	***Corallizoanthus tsukaharai*** **Reimer in Reimer et al., 2008**	1	1	1
		Mesozoanthus Sinniger and Haussermann, 2009	*Mesozoanthus fossii* Sinniger and Haussermann, 2009	2	0	0
		Antipathozoanthus Sinniger et al., 2010	*Antipathozoanthus macaronesicus* (Ocaña and Brito, 2003)	2	0^{a}	0
		Bullagummizoanthus Sinniger et al., 2013	*Bullagummizoanthus emilyacadiaarum* Sinniger et al., 2013	1	0	0
		Hurlizoanthus Sinniger et al., 2013	*Hurlizoanthus parrishi* Sinniger, Ocaña, and Baco, 2013	1	0	0
		Kauluzoanthus Sinniger et al., 2013	*Kauluzoanthus kerbyi* Sinniger et al., 2013	1	0	0

		Kulamanamana Sinniger et al., 2013	*Kulamanamana haumeaae* Sinniger et al., 2013	1	0	0
		Zibrowius Sinniger et al., 2013	*Zibrowius ammophilus* Sinniger et al., 2013	1	0	0
		Umimayanthus Montenegro et al., 2015	***Umimayanthus chanpuru* Montenegro et al., 2015**	3	3	3
	Microzoanthidae	***Microzoanthus*** Fujii and Reimer, 2011	***Microzoanthus occultus* Fujii and Reimer**, 2011	2	2	2
	Nanozoanthidae	***Nanozoanthus*** Fujii and Reimer, 2013	***Nanozoanthus harenaceus* Fujii and Reimer**, 2013	1	1	1
Incertae sedis	**Abyssoanthidae**	***Abyssoanthus*** Reimer and Fujiwara in Reimer et al. 2007	***Abyssoanthus nankaiensis* Reimer and Fujiwara, 2007**	2	2	2
Total taxa				277	28	20

A total number of species
B number of species reported from Japan
C number of species described from Japan
[a]Indicates that although no formally described species was reported from Japan, undescribed species are present

Table 14.2 Zoantharia species reported and described from Japan, and their localities in Japan; taxa in *bold* described from Japan

Species reported from Japan	References from Japan	Localities in Japan
Zoanthus sansibaricus Carlgren, 1900	Ono et al. (2007, 2008), Reimer (2007, 2008, 2010), and Reimer et al. (2006a, 2007c, 2008b, 2011b)	Ryukyu Islands; Satsunan Islands, Kagoshima, Kochi, Wakayama, Ogasawara Islands
***Zoanthus kuroshio* Reimer and Ono, 2006 in Reimer et al., 2006**	Reimer et al. (2006a, 2007c, 2008b, 2011b), Reimer (2007, 2010), and Ono et al. (2008)	Ryukyu Islands, Satsunan Islands, Kagoshima, Kochi, Wakayama, Ogasawara Islands
***Zoanthus gigantus* Reimer and Tsukahara, 2006 in Reimer et al., 2006**	Reimer et al. (2006a, 2007c, 2008b), Reimer (2007, 2010), and Ono et al. (2007, 2008)	Ryukyu Islands, Satsunan Islands, Wakayama, Kochi
Zoanthus aff. *vietnamensis* Pax and Müller, 1957	Reimer (2007, 2010), Ono et al. (2008), and Reimer et al. (2008b)	Ryukyu Islands, Satsunan Islands, Kagoshima, Kochi
Isaurus tuberculatus Gray, 1828	Reimer (2007, 2008, 2010), Reimer et al. (2007c, 2008b, c), and Ono et al. (2008)	Ryukyu Islands, Satsunan Islands, Kochi
Palythoa tuberculosa (Esper, 1805)	Yamazato et al. (1973), Reimer et al. (2006b, 2007b, 2008b, c, 2011b), Ono et al. (2008), Reimer (2008, 2010), Hirose et al. (2011), and Hibino et al. (2013, 2014)	Ryukyu Islands, Satsunan Islands, Kagoshima, Kochi, Wakayama, Miyake-jima, Ogasawara Islands
Palythoa mutuki (Haddon and Shackleton, 1891)	Reimer et al. (2006b, 2007b, 2008b, c, 2011b), Reimer (2007, 2010), and Ono et al. (2008)	Ryukyu Islands, Satsunan Islands, Kagoshima, Kochi, Wakayama, Miyake-jima, Ogasawara Islands
Palythoa heliodiscus (Ryland and Lancaster, 2003)	Reimer (2010), Reimer et al. (2006b, 2007b, 2008b), and Ono et al. (2008)	Ryukyu Islands, Satsunan Islands
***Palythoa mizigama* Irei et al., 2015**	Irei et al. (2015)	Ryukyu Islands
***Palythoa umbrosa* Irei et al., 2015**	Irei et al. (2015)	Ryukyu Islands
Sphenopus marsupialus (Gmelin, 1791)	Reimer et al. (2016a)	Okinawa Island
***Sphenopus exilis* Fujii and Reimer, 2016**	Fujii and Reimer (2016)	Okinawa Island
***Neozoanthus uchina* Reimer et al., 2012**	Reimer (2010), and Reimer et al. (2011a, 2012, 2013a)	Ryukyu Islands, Satsunan Islands
***Epizoanthus indicus* (Lwowsky, 1913)**	Reimer et al. (2010)	East China Sea
***Epizoanthus cnidosus* Tischbierek, 1929**	Tischbierek (1929)	Sagami Bay
Epizoanthus illoricatus Tischbierek, 1930	Kise and Reimer (2016)	Ryukyu Islands

(continued)

Table 14.2 (continued)

Species reported from Japan	References from Japan	Localities in Japan
***Epizoanthus ramosus* Carlgren, 1936**	Carlgren (1934), and Reimer et al. (2010, 2013c)	Sagami Bay, Wakayama
***Epizoanthus inazuma* Kise and Reimer, 2016**	Kise and Reimer (2016)	Ryukyu Islands
Hydrozoanthus gracilis (Lwowsky, 1913)	Lwowsky (1913), Reimer et al. (2006a), and Sinniger et al. (2010)	Sagami Bay
***Corallizoanthus tsukaharai* Reimer**, 2008 **in Reimer et al.**, 2008a	Reimer et al. (2008a)	Ryukyu Islands, Satsunan Islands.
***Umimayanthus chanpuru* Montenegro et al.,** 2015	Montenegro et al. (2015)	Ryukyu Islands, Satsunan Islands, Yamaguchi
***Umimayanthus miyabi* Montenegro et al.,** 2015	Montenegro et al. (2015)	Ryukyu Islands, Satsunan Islands, Kochi
***Umimayanthus nakama* Montenegro et al.,** 2015	Montenegro et al. (2015)	Ryukyu Islands, Kochi
***Microzoanthus occultus* Fujii and Reimer**, 2011	Fujii and Reimer (2011)	Ryukyu Islands, Satsunan Islands, Ogasawara Islands
***Microzoanthus kagerou* Fujii and Reimer**, 2011	Fujii and Reimer (2011)	Ryukyu Islands, Ogasawara Islands, Chiba, Yamagata
***Nanozoanthus harenaceus* Fujii and Reimer**, 2013	Fujii and Reimer (2013)	Okinawa Island
***Abyssoanthus nankaiensis* Reimer and Fujiwara in Reimer et al.**, 2007a	Reimer et al. (2007a)	Nankai Trough (off Muroto, Kochi)
***Abyssoanthus convallis* Reimer and Sinniger**, 2010	Reimer and Sinniger (2010)	Japan Trench (off Sanriku, Iwate)

for its high biodiversity of many coral reef species (Hoeksema 2007), remains largely unexamined (Reimer et al. 2014b), and it is clear that more research in other regions of the world is needed, as has recently been shown for the South China Sea (Reimer et al. 2015).

Here, in this chapter, we focus specifically on the diversity of Zoantharia in Japan. The plan of this chapter is to introduce the diversity of Zoantharia in Japan to readers, while at the same time pointing out areas and regions of potential future research interest. Finally, we give some recommendations for future zoantharian researchers in terms of methodology and protocol.

14.2 Material and Methods in Literature Review

All primary literature on Zoantharia from Japan was examined, and locations of specimens and research noted to as detailed a location as possible. We included all primary literature, but did not include gray literature such as guidebooks or government reports, as identities of many species were questionable or unverifiable. We limited our reports and records in this study to formally described Zoantharia species listed in the World Register of Marine Species (WoRMS Editorial Board 2015), and also double checked as many of the records as possible with the Hexacorallia.com database (Fautin 2013) by searching "Japan" and "list of all scientific names" to show a "list of names and place names" for Zoanthidea (=Zoantharia). A list of literature examined is presented in Table 14.2. Locations were then plotted on a map of Japan to show the relative effort of research within the different areas of Japan (Fig. 14.3). At the same time, zoantharian species reported from Japan were noted, and included within a table with relevant information (Table 14.2).

14.3 Results and Discussion

14.3.1 Zoantharian Diversity in Japanese Waters

In terms of genus-level or higher diversity, the waters around Japan are among the richest in the world for Zoantharia, including 14 of all 27 presently recognized zoantharian genera (=52 % of all genera) (Table 14.1). As well, this number does not include the genera *Terrazoanthus*, *Antipathozoanthus*, and *Parazoanthus* as they are not yet formally recorded from Japan, although undescribed species are present in the waters of Okinawa and Kagoshima, respectively (Reimer et al. 2013c; Reimer and Fujii, unpublished data), which would bring the number to 17 of 27 (~63 %). Overall, such data strongly suggest that Japan is a hotspot of the recorded Zoantharia diversity, at least at the level of genus or higher. However, there are several factors that cast uncertainty on the idea of Japan as a zoantharian-diversity hotspot.

The first impediment to frankly assessing the merit of Japan as a zoantharian-diversity hotspot is the lack of information from surrounding countries and regions. To the west, only one species of zoantharian has been reported from North or South Korea in primary literature (Reimer et al. 2016b). Similarly, from the Chinese portion of the East China Sea, asides from several *Epizoanthus* spp. from the East China Sea mentioned by Zunan (1998), there are almost no data. In the Philippines, although historically important (Gray 1867; Tischbierek 1930), no proper zoantharian-diversity assessment nor almost any recent research has been conducted in the region, whereas the Coral Triangle data consist of a recent detailed examination (Reimer et al. 2014b) plus some records in papers not focused on the region (Sinniger et al. 2005) or only focused on a few taxa (Di Camillo et al. 2010). Detailed species lists have been published covering geographic areas such as Guam (Paulay et al. 2003), Palau (Reimer et al. 2014a), and Taiwan (Reimer et al. 2013b), but all these lists focused only on shallow waters and are mostly incomplete in terms of zoantharian species diversity. Thus, until surveys are more complete for surrounding areas, it is difficult to state with confidence that Japanese waters host an unusually high level of zoantharian diversity.

Furthermore, even though the level of Zoantharia diversity research for Japan is advanced compared to surrounding areas, it is easy to see there is still a serious sampling effort bias (Fig. 14.3). The majority of research has been conducted along the path of the Kuroshio Current, much of it on *Zoanthus* and *Palythoa* species, which have distributions limited by the warm waters of the Kuroshio (Reimer et al. 2008b). Other areas, such as the Sea of Japan, the Inland Sea, and northern Japan (Tohoku region and Hokkaido), are still very understudied, with only one or two specimens or investigations from each area. Thus, even for Japanese waters, it would appear our understanding of Zoantharia diversity is still somewhat nascent.

Furthermore, there are still several known but undescribed species in Japanese waters awaiting formal description (Fig. 14.4), most likely as well as an unknown

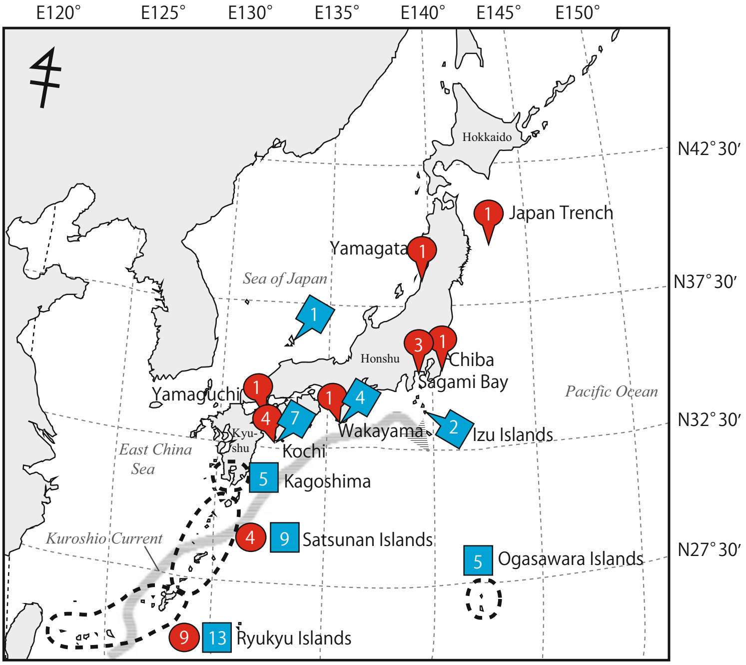

Fig. 14.3 Map showing distributional records of described species of zoantharians in Japan from the literature as described in the Materials and Methods. Numbers of Brachycnemina species at each locality/region shown inside *blue squares*, and Macrocnemina + Abyssoanthidae species inside *red circles*

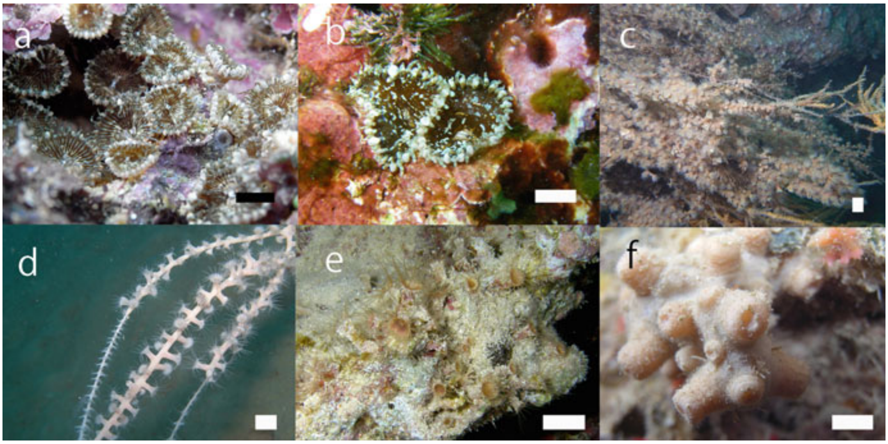

Fig. 14.4 Some undescribed Zoantharia species from Japanese waters. (**a**) *Palythoa* sp. 1. (**b**) *Palythoa* sp. 2. (**c**) *Antipathozoanthus* sp. 1, (**d**) *Antipathozoanthus* sp. 2, (**e**) *Antipathozoanthus* sp. 3, (**f**) *Epizoanthus* sp. 1. Scale bars approximately 10 mm

number of undiscovered and undescribed species. Most known but undescribed species are also from the Kuroshio Region; from caves or cracks in coral reefs (Kise and Reimer 2016), the deep sea, or muddy bays (Reimer and Fujii, unpublished data). Thus, as previously stated (Fujii and Reimer 2011), not only is there a sampling bias on a regional scale, but at the scale of ecosystem or habitat there is also bias. More effort and research are needed for such understudied environments.

In summary, it is clear much more work is needed before we can say with confidence that Japanese waters are highly diverse in terms of Zoantharia. For now, it does appear that the waters around Japan do harbor high levels of Zoantharia biodiversity, as seen in previous studies on other cnidarian taxa (Grossmann and Lindsay 2013), or when assessing overall marine biodiversity (Fujikura et al. 2010).

In conclusion, the following steps need to be taken to advance our understanding of Zoantharia diversity:

1. Surveys of diversity of Zoantharia from regions around Japan (e.g., Korea, coastal China, Coral Triangle)
2. Surveys within Japan in regions that have been neglected thus far (e.g., Sea of Japan, northern Japan, Inland Sea)
3. Surveys in ecosystems that have also been relatively neglected in terms of Zoantharia research (caves and cracks in coral reefs, muddy or sedimented bays, mesophotic and deep-sea ecosystems)

Until such research is undertaken, our knowledge of zoantharian biodiversity will remain incomplete. As zoantharians are known to have potentially important natural products (e.g., palytoxin in Moore and Scheuer 1971; norzoanthamine in Miyashita et al. 2004), and have been implicated in ecosystem phase shifts resulting from changes in the environment (Yang et al. 2013; Cruz et al. 2015), research into understanding their diversity and biogeography are important for the data needed to better predict how future climate changes will impact marine ecosystems.

14.3.2 Future Avenues of Zoantharian Diversity Research

Recent results utilizing the combination of molecular phylogenetic analyses with morphological characteristics have proven useful in reassessing and examining the diversity of Zoantharia, with many new taxa being erected based largely on genetic data (Table 14.1). One potential next step in such analyses is the utilization of combined analyses with associated species (e.g., host species of Macrocnemina, *Symbiodinium* for Brachycnemina), as suggested recently to help further discern between *Umimayanthus* spp. by examining host sponge species using molecular data (Montenegro et al. 2015). Additionally, with common zooxanthellate species such as *Palythoa tuberculosa* that can be the dominant benthos in the shallow coral reefs of Okinawa (Irei et al. 2011; Yang et al. 2013), it appears that they host a large and diverse assemblage of other organisms, including crustaceans (e.g., Xanthidae: Den Hartog and Türkay 1991), nudibranchs (e.g., Aeolidiidae: Rudman 1982; Carmona et al. 2014), mollusks (e.g., Epitoniidae: Zahn 1980), and copepods (e.g., Cyclopoida: Humes and Ho 1966), as well as microbial assemblages (Chimetto et al. 2009). Understanding patterns of association and potential coevolution may help increase our knowledge on how to discern between closely related zoantharian species or groups.

Discerning between closely related groups will be crucial in the future taxonomic research of many Brachycnemina, as it is believed that there is a high rate of synonymy among species caused by inadvertent redescriptions of the same species from different localities or with slightly different morphologies (Burnett et al. 1997), as these groups can have high intraspecific morphological plasticity (Ong et al. 2013). Molecular data indicate for the genera *Palythoa* and *Zoanthus* that the number of species in both groups may be much lower than had been thought in the past (Burnett et al. 1997), and high-resolution molecular markers, microsatellites (Wham et al. 2013), or single-nucleotide polymorphisms (Itoi et al. 2005) combined with the faunal associations just proposed may provide important clues in species identities. When assessing species-level diversity, although only 28 of 277 total worldwide species (=10.1 %; Table 14.1) have been reported from Japan, true species-level diversity remains unclear because of the still chaotic situation surrounding the taxonomy of many species (Burnett et al. 1997). For now, realistic assessments of species-level diversity of Zoantharia in Japan or any other location, and particularly species within Brachycnemina, are still far in the future.

One final potentially beneficial avenue of research to help clarify zoantharian diversity is the linking of molecular data with museum (e.g., type) specimens. Although most type specimens have been preserved in formalin, which damages DNA and the ability to conduct phylogenetic analyses, recent advances with other anthozoan taxa (Baker et al. 2013) indicate it may yet be possible to gain species-level molecular data from such zoantharian specimens. Achieving an accurate and reliable method to examine type specimens may help reconcile and clarify the levels of synonymy within currently problematic genera such as *Palythoa* and *Zoanthus*.

Finally, as the number of active zoantharian taxonomists is somewhat limited on a worldwide scale, as with many other so-called 'minor' taxa, the creation of accurate field identification guides based on information gained from new scientific analyses could help fill in regional gaps in distributions. Particularly, Japan has a large SCUBA-diving and aquarist community with many 'citizen scientists' interested in 'minor' taxa, and providing scientifically proven accurate materials and literature could help expand our knowledge of zoantharians in Japan (and other regions) greatly.

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References

Baker DM, Weigt L, Fogel M, Knowlton N (2013) Ancient DNA from coral-hosted *Symbiodinium* reveal a static mutualism over the last 172 years. PLoS One 8(2):e55057

Burnett WJ, Benzie JAH, Beardmore JA, Ryland JS (1997) Zoanthids (Anthozoa, Hexacorallia) from the Great Barrier Reef and Torres Strait, Australia: systematics, evolution and a key to species. Coral Reefs 16:55–68

Carmona L, Pola M, Gosliner TM, Cervera JL (2014) Review of *Baeolidia*, the largest genus of Aeolidiidae (Mollusca: Nudibranchia), with the description of five new species. Zootaxa 3802 (4):477–514

Carlgren O (1934) Über einige ostasiatische Zoantharien. Ark Zool A 28:1–11

Chimetto LA, Brocchi M, Gondo M, Thompson CC, Gomez-Gil B, Thompson FL (2009) Genomic diversity of vibrios associated with the Brazilian coral *Mussismillia hispida* and its sympatric zoanthids (*Palythoa caribaeorum*, *Palythoa variabilis* and *Zoanthus solanderi*). J Appl Microbiol 106(6):818–1826

Den Hartog JC, Türkay M (1991) *Platypodiella georgei* spec. nov. (Brachyura: Xanthidae), a new crab from the island of St. Helena, South Atlantic Ocean, with notes on the genus *Platypodiella* Guinot, 1967. Zool Med 65:209–220

Di Camillo CG, Bo M, Puce S, Bavestrello G (2010) Association between *Dentitheca habereri* (Cnidaria: Hydrozoa) and two zoanthids. Ital J Zool 77:81–91

Cruz ISC, Loiola M, Albuquerque T, Reis RR, Nunes JACC, Reimer JD, Mizuyama M, Kikuchi RKP, Creed JC (2015) Effect of phase shift from corals to zoanthid on reef fish assemblages. PLoS One 10:e0116944

Fautin DG (2013) Hexacorallians of the world. http://geoportal.kgs.ku.edu/hexacoral/anemone2/index.cfm/. Accessed on 05-09-2015

Fujii T, Reimer JD (2011) Phylogeny of the highly divergent family Microzoanthidae (Anthozoa, Hexacorallia) from the Pacific. Zool Scr 40:418–431

Fujii T, Reimer JD (2013) A new family of diminutive zooxanthellate zoanthids (Hexacorallia: Zoantharia). Zool J Linn Soc 169:509–522

Fujii T, Reimer JD (2016) A new solitary free-living species of the genus *Sphenopus* (Cnidaria: Anthozoa: Zoantharia: Sphenopidae) from Okinawajima Island, Japan. ZooKeys 606:11–24

Fujikura K, Lindsay D, Kitazato H, Nishida S, Shirayama Y (2010) Marine biodiversity in Japanese waters. PLoS One 5(8):e11836

Gray JE (1867) Notes on Zoanthinae, with the descriptions of some new genera. Proc Zool Soc Lond 15:233–240

Grossmann MM, Lindsay DJ (2013) Diversity and distribution of the Siphonophora (Cnidaria) in Sagami Bay, Japan, and their association with tropical and subarctic water masses. J Oceanogr 64:395–411

Hibino Y, Todd P, Ashworth CD, Obuchi M, Reimer JD (2013) Monitoring colony color and zooxanthellae (*Symbiodinium* spp.) condition in the reef zoanthid *Palythoa tuberculosa* in Okinawa, Japan. Mar Biol Res 9:794–801

Hibino Y, Todd PA, Yang SY, Benayahu Y, Reimer JD (2014) Molecular and morphological evidence for conspecificity of two common Indo-Pacific species of *Palythoa* (Cnidaria: Anthozoa). Hydrobiologia 733:31–43

Hirose M, Obuchi M, Hirose E, Reimer JD (2011) Timing of spawning and early development of *Palythoa tuberculosa* (Anthozoa, Zoantharia, Sphenopidae) in Okinawa, Japan. Biol Bull 220:23–31

Hoeksema BW (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. In: Renema W (ed) Biogeography, time and place: distributions, barriers and islands. Springer, Dordrecht, pp 117–178

Humes AG, Ho JS (1966) New lichomolgid copepods (Cyclopoida) from zoanthid coelenterates in Madagascar. Cah Orstom Oceanogr 5:3–47

Itoi S, Nakaya M, Kaneko G, Kondo H, Sezaki K, Watabe S (2005) Rapid identification of eels *Anguilla japonica* and *Anguilla anguilla* by polymerase chain reaction with single nucleotide polymorphism-based specific probes. Fish Sci 71:1356–1364

Irei Y, Nozawa Y, Reimer JD (2011) Distribution patterns of five zoanthid species in Okinawa Island, Japan. Zool Stud 50:426–433

Irei Y, Sinniger F, Reimer JD (2015) Descriptions of two azooxanthellate *Palythoa* (order Zoantharia: subclass Hexacorallia) species from the Ryukyu Archipelago, southern Japan. ZooKeys 478:1–26

Jae J, Choi K, Don Y (2002) Marine animals in Jeju. Daleunsaesang, Seoul [in Korean]

Kise H, Reimer JD (2016) Unexpected diversity and new species of *Epizoanthus* (Anthozoa: Hexacorallia) attached to eunicid worm tubes from the Pacific Ocean. ZooKeys 562:49–71

Lwowsky FF (1913) Revision der Gattung *Sidisia* Gray (*Epizoanthus* auct.). Ein Beitrag zur Kenntnis der Zoanthiden. Zool Jb Syst Ökol Geogr 34:557–614

Miyashita M, Sasaki M, Hattori I, Sakai M, Tanino K (2004) Total synthesis of norzoanthamine. Science 305(5683):495–499

Moore RE, Scheuer PJ (1971) Palytoxin: a new marine toxin from a coelenterate. Science 172 (3982):495–498

Montenegro J, Sinniger F, Reimer JD (2015) Unexpected diversity and new species in the sponge–Parazoanthidae association in southern Japan. Mol Phylogenet Evol 89:73–90

Ono S, Reimer JD, Tsukahara J (2007) Thriving cnidarian community on the volcanic coastline of Sakurajima Taisho Lava Field, southern Japan. Coral Reefs 26:95

Ono S, Reimer JD, Tsukahara J (2008) Survey of zooxanthellate zoanthid diversity in Kagoshima, Japan. Kuroshio Biosphere 4:1–16

Ong DCW, Reimer JD, Todd PA (2013) Morphologically plastic responses to shading in the zoanthids *Zoanthus sansibaricus* and *Palythoa tuberculosa*. Mar Biol 160:1053–1064

Paulay G, Puglisi MP, Starmer JA (2003) The non-scleractinian Anthozoa (Cnidaria) of the Mariana Islands. Micronesica 35:138–155

Reimer JD (2007) Preliminary survey of zooxanthellate zoanthid diversity (Hexacorallia: Zoantharia) from southern Shikoku, Japan. Kuroshio Biosphere 3:1–16, +7 pls

Reimer JD (2008) Implications for different diversity levels of *Symbiodinium* spp. (Dinophyceae, Suessiales) within closely related host genera: zoanthids (Cnidaria: Hexacorallia: Anthozoa) as a case study. Galaxea 10:3–13

Reimer JD (2010) Key to field identification of shallow water brachycnemic zoanthids (order Zoantharia: suborder Brachycnemina) present in Okinawa. Galaxea 12:23–39

Reimer JD, Sinniger F (2010) Discovery and description of a new species of *Abyssoanthus* (Zoantharia: Hexacorallia) at the Japan Trench: the world's deepest known zoanthid. Cah Biol Mar 51:451–457

Reimer JD, Ono S, Iwama A, Tsukahara J, Takishita K, Maruyama T (2006a) Morphological and molecular revision of *Zoanthus* (Anthozoa: Hexacorallia) from southwestern Japan with description of two new species. Zool Sci 23:261–275

Reimer JD, Ono S, Takishita K, Tsukahara J, Maruyama T (2006b) Molecular evidence suggesting species in the zoanthid genera *Palythoa* and *Protopalythoa* (Anthozoa: Hexacorallia) are congeneric. Zool Sci 23:87–94

Reimer JD, Hirano S, Fujiwara Y, Sinniger F, Maruyama T (2007a) Morphological and molecular characterization of *Abyssoanthus nankaiensis*, a new family, new genus and new species of deep-sea zoanthid (Anthozoa: Hexacorallia: Zoantharia) from a northwest Pacific methane cold seep. Invertebr Syst 21:255–262

Reimer JD, Takishita K, Ono S, Maruyama T (2007b) Diversity and evolution in the zoanthid genus *Palythoa* (Cnidaria: Hexacorallia) utilizing nuclear ITS-rDNA. Coral Reefs 26:399–410

Reimer JD, Takishita K, Ono S, Tsukahara J, Maruyama T (2007c) Molecular evidence suggesting intraspecific hybridization in *Zoanthus* (Anthozoa: Hexacorallia). Zool Sci 24:346–359

Reimer JD, Nonaka M, Sinniger F, Iwase F (2008a) Morphological and molecular characterization of a new genus and new species of parazoanthid (Anthozoa: Hexacorallia: Zoantharia) associated with Japanese red coral (*Paracorallium japonicum*) in southern Japan. Coral Reefs 27:935–949

Reimer JD, Ono S, Sinniger F, Tsukahara J (2008b) Distribution of zooxanthellate zoanthid species (Zoantharia: Anthozoa: Hexacorallia) in southern Japan limited by cold temperatures. Galaxea 10:57–67

Reimer JD, Ono S, Tsukahara J, Iwase F (2008c) Molecular characterization of the zoanthid genus *Isaurus* (Anthozoa: Hexacorallia) and its zooxanthellae (*Symbiodinium* spp.). Mar Biol 153:351–363

Reimer JD, Hirose M, Nishisaka T, Sinniger F, Itani G (2010) Epizoanthus spp. associations revealed using DNA markers: a case study from Kochi, Japan. Zool Sci 27:729–734

Reimer JD, Hirose M, Irei Y, Obuchi M, Sinniger F (2011a) The sands of time: rediscovery of the genus *Neozoanthus* (Cnidaria: Hexacorallia) and evolutionary aspects of sand encrustation in brachycnemic zoanthids. Mar Biol 158:983–993

Reimer JD, Hirose M, Yanagi K, Sinniger F (2011b) Marine invertebrate diversity in the oceanic Ogasawara Islands: a molecular examination of zoanthids (Anthozoa: Hexacorallia) and their *Symbiodinium* (Dinophycaea). Syst Biodivers 9:133–144

Reimer JD, Irei Y, Fujii T (2012) Two new species of *Neozoanthus* (Cnidaria, Hexacorallia, Zoantharia) from the Pacific. ZooKeys 246:69–87

Reimer JD, Irei Y, Naruse T (2013a) A record of *Neozoanthus* cf. *uchina* Reimer, Irei & Fujii, 2012 from the Yaeyama Islands, southern Ryukyu Islands, Japan. Fauna Ryukyuana 7:1–7

Reimer JD, Irei Y, Fujii T, Yang SY (2013b) Phylogenetic analyses of shallow water zoanthids (Cnidaria: Hexacorallia) and their *Symbiodinium* spp. from Taiwan. Zool Stud 52:38 [16 pp]

Reimer JD, Sinniger F, Irei Y (2013c) Preliminary list of macrocnemic zoanthid diversity (Anthozoa: Hexacorallia: Zoantharia) from southern Shikoku, Japan. Kuroshio Biosphere 9:1–X + 2 pls

Reimer JD, Albinsky D, Yang SY, Lorion J (2014a) Zoanthid (Cnidaria: Anthozoa: Hexacorallia: Zoantharia) species of coral reefs in Palau. Mar Biodivers 44:37–44

Reimer JD, Poliseno A, Hoeksema BW (2014b) Shallow-water zoantharians (Cnidaria, Hexacorallia) from the Central Indo-Pacific. ZooKeys 444:1–57

Reimer JD, Wee HB, Put A Jr, Hoeksema BW (2015) Zoantharia (Cnidaria: Anthozoa: Hexacorallia) of the South China Sea and Gulf of Thailand: species list based on past reports and new photographic records. Raffles Bull Zool 63:334–356

Reimer JD, Higashiji T, Nonaka M (2016a) First record of the genus *Sphenopus* (Anthozoa: Hexacorallia: Zoantharia) from Japan. Fauna Ryukyuana 29:37–40

Reimer JD, Kim S, Arai S, Keshavmurthy S, Choi K-S (2016b) First records of zooxanthellate Zoanthus (Anthozoa: Hexacorallia: Zoantharia) from Korea and Japan (East) Sea. Mar Biodiv (in press)

Rudman WB (1982) The taxonomy and biology of further aeolidacean and arminacean nudibranch molluscs with symbiotic zooxanthellae. Zool J Linn Soc 74:147–196

Ryland JS, Lancaster JE (2004) A review of zoanthid nematocyst types and their population structure. Hydrobiologia 530-531:179–187

Sinniger F, Montoya-Burgos JI, Chevaldonne P, Pawlowski J (2005) Phylogeny of the order Zoantharia (Anthozoa, Hexacorallia) based on the mitochondrial ribosomal genes. Mar Biol 147:1121–1128

Sinniger F, Reimer JD, Pawlowski J (2010) The Parazoanthidae DNA taxonomy: description of two new genera. Mar Biodivers 40:57–70

Tischbierek H (1929) Eine neue *Epizoanthus*-Art aus den Japanischen Gewässern (*Epizoanthus cnidosus* n. sp.). Zool Anz 85:28–33

Tischbierek H (1930) Zoanthiden auf Wurmröhren. Zool Anz 91:91–95

Uchida H, Soyama I (2001) Sea anemones in Japanese waters. TBS Britannica, Tokyo

Wham D, Carmichael M, Reimer JD, LaJeunesse T (2013) Eight polymorphic microsatellite loci for the Indo-Pacific wide zoanthid, *Zoanthus sansibaricus*. Mar Biodivers 43:247–250

WoRMS Editorial Board (2015) World register of marine species. Available from http://www.marinespecies.org at VLIZ. Accessed 8 May 2015

Yamazato K, Yoshimoto F, Yoshihara N (1973) Reproductive cycle in a zoanthid *Palythoa tuberculosa* Esper. Proceedings of 2nd international symposium on the Cnidaria. Seto Marine Biology Laboratory, Kushimoto, pp 275–283

Yang SY, Ashworth CD, Bourgeois C, Reimer JD (2013) *Palythoa* zoanthid "barrens" in Okinawa: examination of possible environmental causes. Zool Stud 52:39 [11 pp]

Zahn LP (1980) Living together in the sea. TFH Publications, Neptune

Zunan P (1998) Coelenterata Actiniaria Ceriantharia Zoanthidea. Science Press, Beijing

Chapter 15
Diversity and Morphological Adaptation of Dicyemids in Japan

Hidetaka Furuya

Abstract Dicyemid mesozoans (phylum Dicyemida) are the most common and characteristic endosymbionts found in the renal sac of benthic cephalopod mollusks, a unique environment in which they spend most of their life. Dicyemids have a distinct anterior region termed a 'calotte' by which they attach to the renal appendages of the host: it is a key structure for survival in the renal sac. About 50 species have been recognized in 25 species of cephalopods in Japan. Typically, 2 or 3 dicyemid species are found in individuals of each cephalopod species and most are host specific. There is an interesting relationship between the calotte configuration and the co-occurrence pattern in cephalopod hosts. Four basic types of calotte shape are recognized among dicyemid species. Calotte shapes in different dicyemid species from different host species may often more closely resemble each other than that of other species of dicyemid in the same host individual, when it harbors more than two dicyemid species. Multiple species of dicyemids appear to be able to coexist in the renal sac without competition when the shapes of their calottes are different: dicyemids with conical or dome-shaped calottes are found within the convolutions or folds of the renal appendages, whereas species with flat, discoidal calottes attach to the surface of the renal appendages. Interspecific competition is most likely avoided by habitat segregation among dicyemids possessing different calotte shapes.

Keywords Adaptive radiation • Convergence • Morphological adaptation • Dicyemida • Dicyemids • Endosymbiont • Mesozoa

15.1 Introduction

Every animal species harbors at least one species of parasite or symbiont. Dicyemid mesozoans (phylum Dicyemida) are the commonest and most characteristic endosymbionts of benthic cephalopod mollusks, namely, octopuses and cuttlefishes

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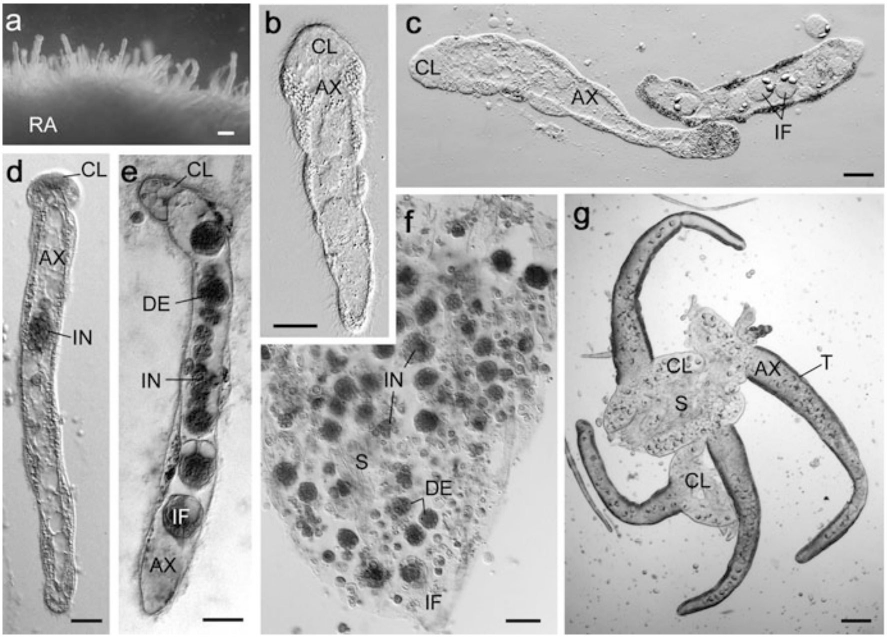

Fig. 15.1 Dicyemids on the renal appendage of *Amphioctopus fangsiao* (**a**) and diversity of dicyemid species (**b–g**). **b** *Dicyema misakiense*. **c** *D. erythrum*. **d** *D. japonicum*. **e** *D. acuticephalum*. **f, g** *Dicyemennea* sp. Note that *Dicyema* sp. has an irregular anterior region that spread, connected with other individuals (**g**), and formed a thin synctium sheet (**f**). **a–c, g** Living specimens; **d–f** specimens stained with Erlich's hematoxylin and eosin. *AX* axial cell, *CL* calotte, *DE* developing infusoriform embryo, *IF* infusoriform embryo, *IN* infusorigen, *RA* renal appendage, *S* syncytium, *T* trunk. *Bars* **b–f** 20 μm; **a**, **g** 50 μm

(Fig. 15.1). A total of about 120 species of dicyemids have been reported in at least 50 species of cephalopods distributed in a variety of geographic localities: the Okhotsk Sea, Japan Sea, western and eastern North Pacific Ocean, waters around New Zealand, North Indian Ocean, Mediterranean, western North and eastern Atlantic Ocean, Gulf of Mexico, and Antarctic Ocean.

The cephalopod fauna of the world comprises approximately 700 species. Currently, at least 150 species are recognized to live in Japanese waters (Sasaki 1929; Kubodera and Lu 2002; Jereb and Roper 2005, 2010; Okutani 2005; Jereb et al. 2014). The coastal and oceanic areas off the Japanese Archipelago comprise a diverse variety of environments stretching from north to south, influenced by such ocean currents as the Kuroshio, Oyashio, and Tsushima Currents. Thus, the marine fauna of Japan is closely associated with the Okhotsk–Bering Sea elements and also with the Indo–West-Pacific elements, which have the highest marine biodiversity in the world.

In cephalopods, the excretory organs are the renal complex (renal and pancreatic appendages) and the branchial heart complex (branchial heart and pericardial appendage). Before release, urine is collected in a renal sac, the fluid-filled coelom of which is a unique environment providing living space for a diversity of endosymbionts, including the parasitic but phylogenetically distant chromidinid ciliates and dicyemids (Hochberg 1982; Furuya et al. 2004a, b). This renal sac environment is particularly suited to the establishment and maintenance of dicyemids (Hochberg 1982, 1983, 1990), the species diversity and morphological adaptations of which are the subject of this review chapter.

15.2 Morphology and Phylogeny

Dicyemids have a simple body consisting of a central cylindrical cell called the axial cell and a single layer of 8–30 ciliated external cells called the peripheral cells (Fig. 15.2). This organization does not correspond to metazoan two-layered construction of endoderm and ectoderm, and dicyemids have neither body cavities nor differentiated organs. Beneden (1876) proposed the name Mesozoa for them to signify their intermediate position between the Protozoa and Metazoa in body organization. Subsequently, Hyman (1940, 1956) and Lapan and Morowitz (1975) also concurred that dicyemids are primitive multicellular organisms. Because dicyemids have several protozoan-like features, an affinity to the protozoans has been pointed out (Awata et al. 2005, 2006; Czaker 2000, 2006; Noto et al. 2003; Noto and Endoh 2004). However, several zoologists regard the simple organization of dicyemids to be the result of specialization for parasitism (Nouvel 1947; Stunkard 1954; Ginetsinskaya 1988). Analysis of molecular sequences has revealed that, rather than truly primitive animals that deserve the name ‘mesozoan,’ they probably belong to the lophotrochozoans (Katayama et al. 1995; Kobayashi et al. 1999; Aruga et al. 2007; Suzuki et al. 2010). Despite their extremely reduced body plan, dicyemids still appear to exhibit some degree of cell differentiation (Ogino et al. 2011). It still remains to be explored how such a simple body organization has evolved.

15.3 Dicyemid Fauna in Japan

The phylum Dicyemida includes three families: Conocyemidae, Dicyemidae, and Kantharellidae. The number of peripheral cells is species specific and constant in the families Conocyemidae and Dicyemidae. The genus *Kantharella* contains only one species, which is characterized by a variable number of peripheral cells (Czaker 1994). At the anterior region of dicyemids, two to ten peripheral cells form the calotte (Fig. 15.3). Dicyemid genera are characterized and identifiable by the number and orientation of cells in each tier of the calotte (Fig. 15.4) (Nouvel 1947; McConnaughey 1949a, b; Hochberg 1990; Furuya et al. 2007). The vermiform and infusoriform larvae typically have a constant number of peripheral cells,

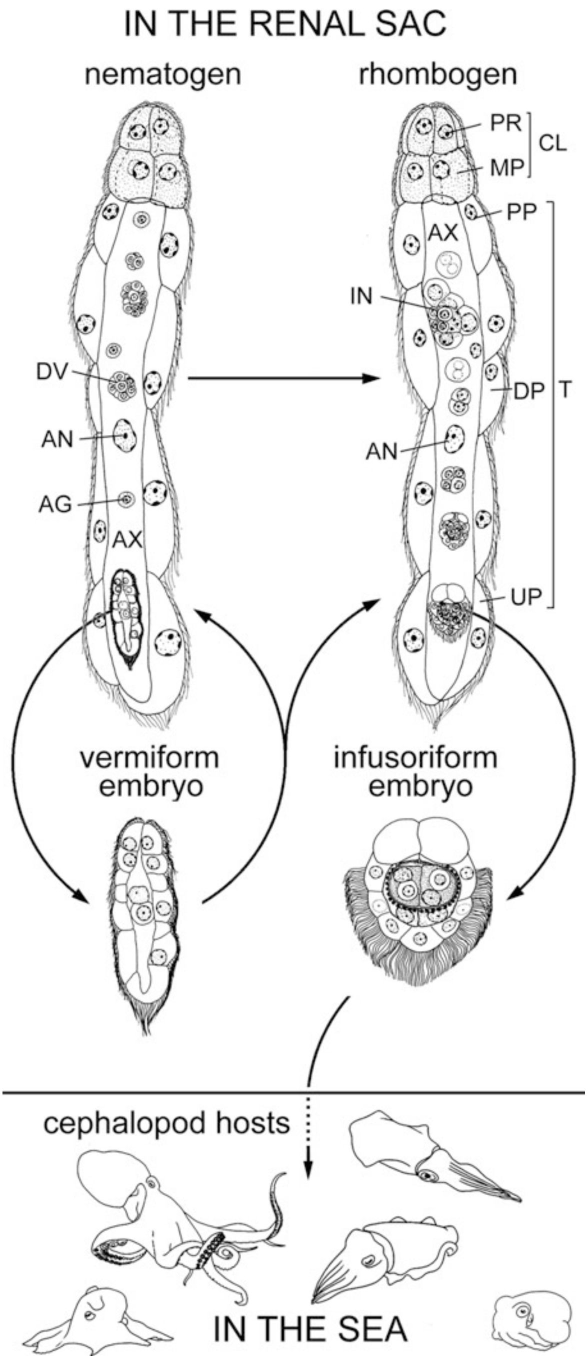

Fig. 15.2 Dicyemid life cycle (modified from Furuya and Tsuneki 2003). The *dashed line* indicates an unknown process involved in the infection of a new cephalopod and development into adult forms. In vermiforms (nematogen, rhombogen, vermiform embryo), a large cylindrical axial cell is surrounded by peripheral cells. Four to ten anterior peripheral cells (propolars and metapolars) form a calotte. The other peripheral cells are diapolars. Two posterior diapolar cells are somewhat specialized as uropolars. The development of infusorigens (hermaphroditic gonads), gametogenesis around the infusorigen and development of two types of embryos all proceed within the cytoplasm of the axial cell. *AG* agamete, *AN* axial cell nucleus, *AX* axial cell, *CL* calotte, *DP* diapolar cell, *DV* developing vermiform embryo, *IN* infusorigen, *MP* metapolar cell, *PP* parapolar cell, *PR* propolar cell, *T* trunk, *UP* uropolar cell

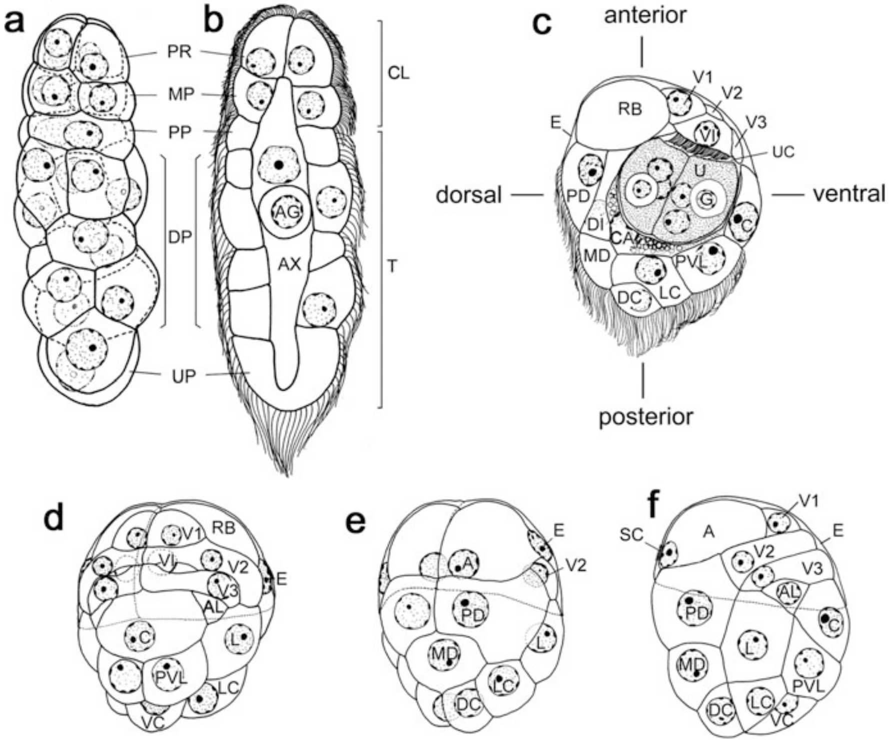

Fig. 15.3 Generalized schematic drawings of vermiform larvae with 22 peripheral cells (**a**, **b**) and infusoriform larvae with 39 cells (**c**–**f**) (modified from Furuya and Tsuneki 2003). **a**, **f** Lateral view. **b**, **c** Sagittal section. **d** Ventral view. **e** Dorsal view. *A* apical cell, *AG* agamete, *AL* anterior lateral cell, *AX* axial cell, *C* couvercle cell, *CA* capsule cell, *CL* calotte, *DC* dorsal caudal cell, *DI* dorsal internal cell, *DP* diapolar cell, *E* enveloping cell, *G* germinal cell, *L* lateral cell, *LC* lateral caudal cell, *MD* median dorsal cell, *MP* metapolar cell, *PD* paired dorsal cell, *PP* parapolar cell, *PR* propolar cell, *PVL* posteroventral lateral cell, *RB* refringent body, *SC* short cilia, *T* trunk, *U* urn cell, *UC* urn cavity, *UP* uropolar cell, *VC* ventral caudal cell, *VI* ventral internal cell, *V1* first ventral cell, *V2* second ventral cell, *V3* third ventral cell

which is species specific (Furuya et al. 2004a, 2007); this is a significant character that can be used to separate species of dicyemids.

The first record of dicyemids in Japan was that of Nouvel and Nakao (1938), describing two new species: *Dicyema misakiense* from *Octopus vulgaris* Lamarck, 1798; and *D. orientale* from *Sepioteuthis lessoniana* Férussac in Lesson, 1831. Later, Nouvel (1947) described the new species *Dicyema acuticephalum* from *Octopus vulgaris* and identified a dicyemid species from *Sepia esculenta* Hoyle, 1885, as *Pseudicyema truncatum* Whitman, 1883, which had been described earlier in Europe. In a subsequent study, the latter species was described as a new species, *Pseudicyema nakaoi* (Furuya 1999). *O. vulgaris*, the common octopus, is considered to inhabit the Mediterranean Sea and the Atlantic coasts: the eastern Atlantic coast from southern England to southwestern Africa, the Azores, the Canary

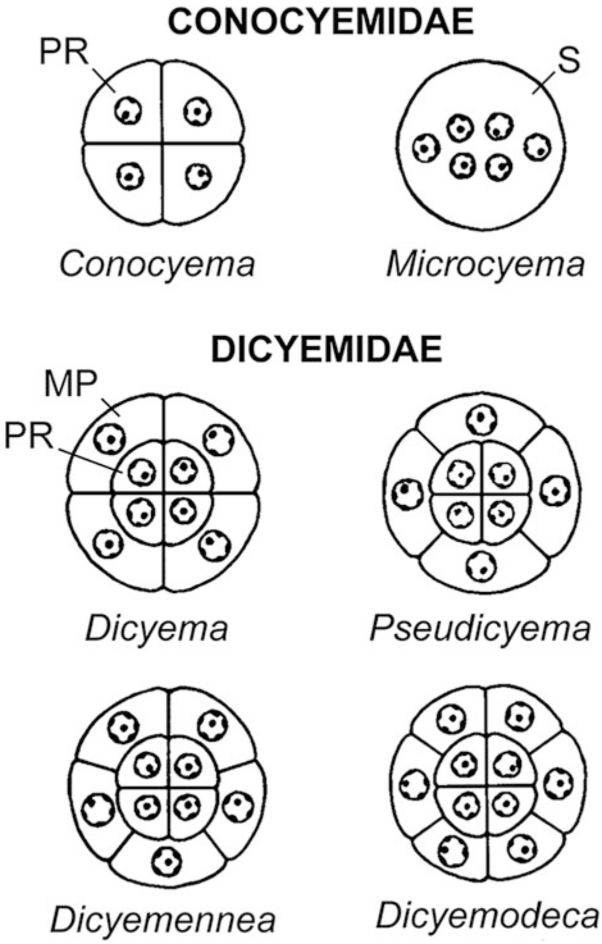

Fig. 15.4 En face views of the calottes of six valid genera of two families (Conocyemidae, Dicyemidae) of Dicyemida. *MP* metapolar cell, *PR* propolar cell, *S* syncytium

Islands, the Cape Verde Islands, the St. Helena Islands; and many localities from the western Atlantic (Mangold 1998; Norman 2000). Norman (2000) suggested that the Japanese common octopus is a different species because of its geographic isolation from *O. vulgaris* of the Mediterranean and Atlantic. The dicyemid fauna is actually distinct in each population of octopus (Nouvel 1947; Furuya et al. 1992a, b). I have surveyed Japanese cephalopods, and to date 39 species of dicyemids have been reported in 16 species of cephalopods in Japan (Table 15.1).

About 50 species of dicyemids have been recognized to date in at least 25 species of cephalopods in Japan (Table 15.1). Many new species of dicyemids are expected to occur in more than 70 potential host species that have been reported to occur in Japanese waters and have yet to be examined.

Table 15.1 Cephalopod and dicyemids species in Japan

Cephalopods	Dicyemids	References
Octopodiformes		
Amphioctopus areolatus	*Dicyema balanocephalum* Furuya, 2006	Furuya (2006c)
	Dicyema leiocephalum Furuya, 2006	
A. fangsiao	*Dicyema colurum* Furuya, 1999	Furuya (1999) and Furuya (2006a)
	Dicyema erythrum Furuya, 1999	
	Dicyema akashiense Furuya, 2006	
	Dicyema awajiense Furuya, 2006	
	Dicyema helocephalum Furuya, 2006	
A. kagoshimensis	*Dicyema irinoense* Furuya, 2005	Furuya (2005)
	Dicyema tosaense Furuya, 2005	
	Dicyema sphaerocephalum Furuya, 2005	
Octopus dofleini	*Dicyemennea nouveli* McConnaughey, 1949	McConnaughey (1949b) and Furuya (1999),
	Dicyemodeca anthinocephalum Furuya, 1999	Furuya (2008b)
O. hongkongensis	*Dicyemennea gyrinodes* Furuya, 1999	Furuya (1999)
	Dicyemennea trochocephalum Furuya, 1999	
	Dicyemennea ophioides Furuya, 1999	
O. minor	*Dicyema clavatum* Furuya and Koshida, 1992	Furuya (1999) and Furuya et al. (1992a)
	Dicyema sphyrocephalum Furuya, 1999	
	Dicyema dolichocephalum Furuya, 1999	
O. sasakii	*Dicyema shimantoense* Furuya, 2008	Furuya (2008c)
	Dicyema codonocephalum Furuya, 2008	
	Dicyema pileum Furuya, 2008	
O. longispadeceus	*Dicyema* sp. 1	
	Dicyema sp. 2	
	Dicyemennea sp. 3	
	Dicyemennea sp. 4	
	Dicyemennea sp. 5	
	Dicyemennea sp. 6	
O. vulgaris	*Dicyema misakiense* Nouvel and Nakao, 1938	Nouvel and Nakao (1938) and Nouvel (1947),
	Dicyema acuticephalum Nouvel, 1947	Furuya et al. (1992a)
	Dicyema japonicum Furuya and Tsuneki, 1992	
Opisthoteuthis depressa	*Dicyemennea umbraculum* Furuya, 2009	Furuya (2009)
Decapodiformes		
Rossia pacifica	*Dicyemennea rossiae* Bogolepova-Dobrokhotova, 1962	Bogolepova-Dobrokhotova (1962),
	Dicyemennea brevicephaloides Bogolepova-Dobrokhotova, 1962	Hoffman (1965) and Furuya (2007)

(continued)

Table 15.1 (continued)

Cephalopods	Dicyemids	References
Sepiella japonica	*Dicyema sepiellae* Furuya, 2008	Furuya (2008a)
Sepia esculenta	*Dicyema hadrum* Furuya, 1999	Furuya (1999)
	Dicyema rhadinum Furuya, 1999	
	Dicyemennea mastigoides Furuya, 1999	
	Dicyemennea minabense Furuya, 1999	
	Pseudicyema nakaoi Furuya, 1999	
S. latimanus	*Dicyemennea ryukyuense* Furuya, 2006	Furuya (2006b)
S. longipes	*Dicyema oxycephalum* Furuya, 2009	Furuya (2009)
	Pseudicyema cappacephalum Furuya, 2009	
S. lycidus	*Dicyema lycidoeceum* Furuya, 1999	Furuya (1999)
Sepioteuthis lessoniana	*Dicyema orientale* Nouvel and Nakao, 1938	Nouvel and Nakao (1938),
	Dicyema koshidai Furuya and Tsuneki, 2005	Furuya and Tsuneki (2005)

15.4 Life Cycle and Reproductive Strategy

Generally, dicyemids have a high prevalence in their host cephalopods and are usually found to be heavily infecting the renal organs (Furuya et al. 2004b). No damage has ever been observed in the infected renal tissue, so dicyemids apparently do no harm to their cephalopod hosts. Lapan (1975) has even suggested that dicyemids facilitate host excretion of ammonia by contributing to acidification of the urine. In addition to the normal muscular contraction of the renal appendages, the ciliary activity of dicyemids present in the kidneys maintains a constant flow of urine, and as a result dicyemids assist in removal of urine. Thus, dicyemids are symbiotic, rather than parasitic, in their relationship with cephalopods.

Dicyemids most likely evolved from free-living ancestors (Hyman 1940; Nouvel 1947; Stunkard 1954) with a direct life cycle of several generations in the same host renal organ. The complicated diphasic life cycle of dicyemids, with a characteristic asexual phase, probably evolved as an adaptation to parasitism (Fig. 15.2), presumably to enable them to adapt to their unique habitat in the host renal organs.

Similar to many endoparasites, the life cycle of dicyemids consists of two phases of different body organization (Nouvel 1947; McConnaughey 1951): (1) the vermiform stage, in which the dicyemid exists as a vermiform embryo formed asexually, and as a final form, the nematogen or rhombogen; and (2) the infusoriform embryo that develops from a fertilized egg. A high population density of dicyemids in the cephalopod kidney may trigger the shift from asexual to sexual reproduction (Lapan and Morowitz 1975). The vermiform stage is restricted to the renal sac of cephalopods, whereas the infusoriform embryos represent a free-living stage, which escape from the host into the sea to search for a new host. However, it is not understood how infusoriform larvae develop into the vermiform stage in the new host.

Asexual reproduction is observed in many endoparasitic groups, including protozoans (Grell 1956; Hochberg 1990; Smyth 1994), cestodes (Hyman 1940, 1949; Stunkard 1975; Rohde 1993), trematodes (Hyman 1940, 1949; Stunkard 1975; Rohde 1993), and orthonectids (Kozloff 1990). The similarity in alternation of sexual and asexual generations has prompted postulation of a close phylogenetic relationship between trematodes and dicyemids (Stunkard 1954; Bogolepova-Dobrokhotova 1963; Ginetsinskaya 1988). However, comparisons of 18S rRNA nucleotide sequences in the dicyemids and other taxa have shown these groups to have separate origins (Powlowski et al. 1996; Katayama et al. 1995). Asexual reproduction in all the aforementioned four groups of parasites seems to have developed independently in each lineage. In these endoparasites, asexual reproduction appears to be an adaptation for similar niches in different hosts. In aquatic animals, taxa with small adults are commonly brooders with embryos held on or in the adult body. However, in species with larger adults, offspring typically are either not cared for or are released at an earlier stage (Strathmann 1990). Adult dicyemids are small in size and embryos are formed within the adult body. When fully grown, the embryos are released. This essentially equates to brooding. Brooding is common among colonial animals that are composed of many small modules (Strathmann and Strathmann 1982), although brooding style is diverse among bryozoans, pterobranch hemichordates, compound ascidians, and several kinds of hard and soft corals. A population or community of dicyemids formed in the renal sac is similar to a colony, although individuals are monozoic (Furuya et al. 2003b).

In dicyemids, the community may develop from a small number of individuals (one or a few) at the initiation of the infection of the renal sac because success of infecting new nongregarious hosts is apparently low at the level of individual infusoriforms. Dicyemids occasionally are found in only one of the two renal sacs in a host octopus. Two different dicyemid species are occasionally detected, one each in the right and left renal sacs of respective hosts (Furuya et al. 1992a; Furuya 2006a). These instances suggest that only a small number of propagules may infect an individual host. Subsequent asexual multiplication forms a large population in the renal sac. Under such conditions, cross-fertilization is of little advantage. Thus, dicyemids might undergo self-fertilization via a hermaphroditic gonad.

15.5 Co-occurrence Pattern and Morphological Adaptation

The majority of the dicyemid species studied were found to be host specific (Furuya 1999). Typically, two or more species of dicyemids are present in each host species or each host individual (Table 15.1). There is an interesting relationship between

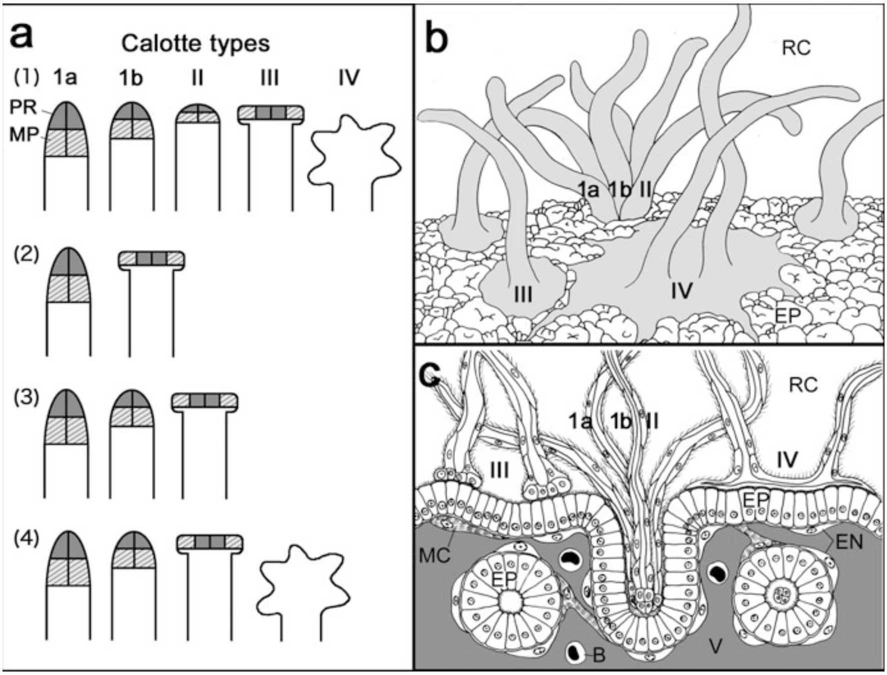

Fig. 15.5 Calotte shapes usually detected within host individual host (**a**), schematic drawings of a surface of renal appendage (**b**), and a cross section of renal appendage (**c**). (*1*) Stylized drawings of the main three types of regular calotte configurations and a type of irregular configuration found in vermiform stages. Type I, conical shape, is divided into two types (type Ia and Ib); type II, cap shaped; type III, discoidal; type IV, an irregular configuration. *Shaded and striped areas* indicate propolar cells and metapolar cells, respectively. (*2*) When two species of dicyemids are present, two distinct calotte shapes, conical and discoidal, are usually observed. (*3*) When three species of dicyemids are present, three types of calotte configurations are usually observed, conical (two grades) and discoidal. (*4*) When more than four species of dicyemids are present, at least one species is characterized by its rare irregularly shaped calotte that spreads, connects with other individuals, and forms a syncytium. *B* blood cell, *EN* endothelium, *EP* epidermal cell of renal appendage, *MC* muscular cell, *RC* renal coelom, *V* vena cava

the calotte configuration of vermiform stages and the co-occurrence pattern in hosts (Fig. 15.5). Vermiform individuals live specifically within the renal sac. Their anterior region, termed a ‘calotte,’ is critical in adapting to their habitats in the renal sac. They insert the distinct anterior region into renal tubules or crypts of the renal appendages of the host (Ridley 1968; Furuya et al. 1997), or attach to surfaces of the renal appendages with a flat anterior region (Furuya et al. 2003a; Furuya 2005, 2006a) (Fig. 15.5b).

When dicyemid species co-occur, their calotte shapes are distinctly different (Furuya et al. 2003a). Four basic types of calotte shape are recognized among 61 species of dicyemids (Fig. 15.5a). A given species usually co-occurs with more than 1 dicyemid species. A regularly shaped, conical calotte (type I) is by far the most typical configuration observed. Dicyemids with a discoidal calotte (type III) are frequently found together with species having a cone-shaped calotte. Calottes that are cap shaped (type II) appear to be intermediate in shape between the conical- and discoidal-type calottes, and tend to occur in the cephalopods when more than 2 species of dicyemids are present. Dicyemids with irregularly shaped bodies and calottes (type IV) occur when more than 3 species coexist. When more than 2 dicyemid species are present in a single host individual, calotte shapes are dissimilar as a rule. Calotte shapes in dicyemid species from different host species more closely resemble each other than those of dicyemids observed within the same host species.

Different dicyemid species possessing similar calotte shapes are very rarely found together in a single host individual, and in all such cases one species is usually dominant. In these cases, the most adaptive species for the habitat possibly becomes a dominant and niche-occupying species. Thus similar types of dicyemids rarely, if ever, share the same renal sac, because one dicyemid species already occupies the niche required by the other species. In the Japanese *Octopus vulgaris*, two species of dicyemids, namely, *Dicyema acuticephalum* and *D. misakiense*, possess similar calotte types. In more than 150 specimens of this octopus species examined, these two species were never found together (Furuya et al. 2003a). The Atlantic pygmy octopus, *Octopus joubini*, harbors two dicyemid species, *Dicyema apalachiensis* and *D. hypercephalum*, which have very similar calotte shapes and also were never found together in the same host individual. In these cases, the best adapted species for the habitat presumably shows the highest prevalence among dicyemids and, therefore, it arises as a dominant species in such host species. In a host individual, interspecific competition between dicyemids may result when they have similar calotte shapes, and these dicyemids tend to infect different host individuals (Furuya et al. 2003a).

Different species of dicyemids appear to be able to coexist in the renal sac without competition when their calottes are different in shape. Dicyemids with discoidal calottes typically are found together with dicyemids possessing a conical calotte. For instance, *Dicyema misakiense* (conical) and *D. japonicum* (discoidal) inhabit different regions of the renal organs (Furuya et al. 2003a). In general, dicyemids with conical calottes (type I) insert the anterior region of the body into crypts or folds in the renal appendages. In contrast, dicyemids with cap-shaped (type II) or disc-shaped calottes (type III) attach to the broad, flat, or gently rounded surfaces of the renal appendages (Fig. 15.5c). Interspecific competition is most likely avoided by habitat segregation in dicyemids that possess different calotte shapes. As a consequence, species of dicyemids with different calotte configurations are able to coexist in the renal sacs of a single host individual. Although these instances occur with a frequency similar to those when only one species is present, these observations do not necessarily contradict the habitat segregation hypothesis because of the possible absence of infection of another species in the latter, or another niche might simply be vacant. Calotte morphology in dicyemids appears to result from adaptation to the structure of the hosts' renal tissues and helps to facilitate niche separation of coexisting species.

Dicyemids that have similar calotte shapes, such as *Dicyema acuticephalum* and *D. misakiense,* have never been found together. However, when *Dicyema japonicum* is present, these two species are able to coexist in the same renal habitat. The presence of *D. japonicum* may reduce the competition between *D. acuticephalum* and *D. misakiense*. Similarly, the presence of unusual dicyemids with irregularly shaped calottes and bodies (type IV) may reduce competition between dicyemids with other calotte and body configurations. Although it is unknown how type IV dicyemids attach to the renal organs, most likely they adhere to the surface of the renal appendages, as do dicyemids with discoidal calottes.

Calottes are typically conical in shape in vermiform embryos of almost all species and in adult vermiform stages of most species (Furuya et al. 2001, 2007). A conical calotte is thus the most commonly, or frequently, observed configuration in dicyemids. This shape is formed simply by proportional cell enlargement. In the process of ontogenetic growth from embryo to adult, the shape of the calotte changes from conical via cap shaped to discoidal. The cap-shaped calotte appears to be intermediate between what might be termed the plesiomorphic, or primitive, condition (conical calotte configuration) and a more advanced or apomorphic discoidal configuration. In the developmental process a disc-shaped calotte represents the hypermorphic state. The conical shape is possibly an original form of larval type among dicyemids. Thus, cap- and disc-shaped calotte configurations are formed secondarily and are therefore derived from the conical-shaped calotte. Consequently, various morphological characters might have been selected to reduce competition in each different host species as a result of heterochrony.

In Japan, *Dicyema misakiense* and *D. japonicum* are often found together in the same host individual. Nouvel and Nakao (1938) did not differentiate them as distinct species because of their general morphological similarities. Cell lineages in both vermiform larvae and infusorigens, and the numbers and types of cells in infusoriform larvae, are identical (Furuya et al. 1992a, 1993, 1994, 2004a). The principal difference between these species is calotte shape, and an intermediate shape is never found (Furuya et al. 1992b). As far as morphological characters are concerned, these two species are considered to be closely related, but different species. In such sympatric, congeneric species of dicyemids, morphological character displacement may occur to increase differences between species; this may be associated with speciation in dicyemids.

Among dicyemids found in different cephalopod host species and with different geographic distributions (both horizontal and vertical), the developmental patterns and cell lineages of vermiform embryos are highly conserved and the morphology of embryos is little modified (Furuya et al. 2001). Such conservative developmental features can be attributed to the seemingly uniform microhabitat present in the inside of the axial cells of the parent nematogens. Morphological changes principally occur in the renal sac following release from the constraints of the restrictive microhabitat found in the axial cell of the parent. After eclosion, dicyemids might adapt to the surface structure of renal organs. When several species of dicyemids are present within the renal sac of a single host individual, interspecific interactions likely occur, and competitive exclusion may select for character displacement and habitat segregation: this is an example of niche separation in organisms possessing a similar lifestyle.

15.6 Cephalopod Renal Organs as a Microhabitat for Small Animals

Molecular studies have revealed close relationships of dicyemid species coexisting in one host species, with examples observed in *Amphioctopus fangsiao*, *Octopus vulgaris*, and *O. hongkongensis* (Furuya, unpublished data). This finding is interpreted as meaning that sympatric speciation has occurred in the same host species. An ancestral species of dicyemids appears to have given rise to multiple species, which exploit different niches such as crypts and surfaces in the renal appendages. This situation is reminiscent of a famous model for speciation and adaptive radiation: Darwin's finches inhabiting the Galápagos Islands and the Cocos Islands. The renal organs of cephalopods correspond to 'islands.' A single species of dicyemid found its way to the renal organ of a certain cephalopod species and adaptively specialized to this particular environmental niche. As a result, the calotte configurations of dicyemids show convergence when compared across different host cephalopod species (Fig. 15.6).

Dicyemids are subject to a number of selection pressures because of their unique habitat within the kidneys of their cephalopod hosts. In terms of morphological and ecological adaptation, this microenvironment seems to have provided the laboratory space for a simple natural experiment.

Acknowledgments I sincerely thank Dr. Kazuhiko Tsuneki and the late Dr. Yutaka Koshida for introducing us to a fascinating world of dicyemids. Thanks are also due to Dr. F.G. Hochberg for providing an opportunity to study dicyemids from a global aspect. I also thank Dr. Ian G. Gleadall for providing me with updated information on current octopus taxonomy. I am grateful to Ms. Fuko Onoda for the assistance with this work. The studies summarized in this review were supported by grants from the Fujiwara Natural History Foundation, the Nakayama Foundation for Human Science, the Research Institute of Marine Invertebrates Foundation, the Inamori Foundation, the Toray Science Foundation, and Grants-in-Aid for Scientific Research of the Japan Society for the Promotion of Science (research grant no. 26440216).

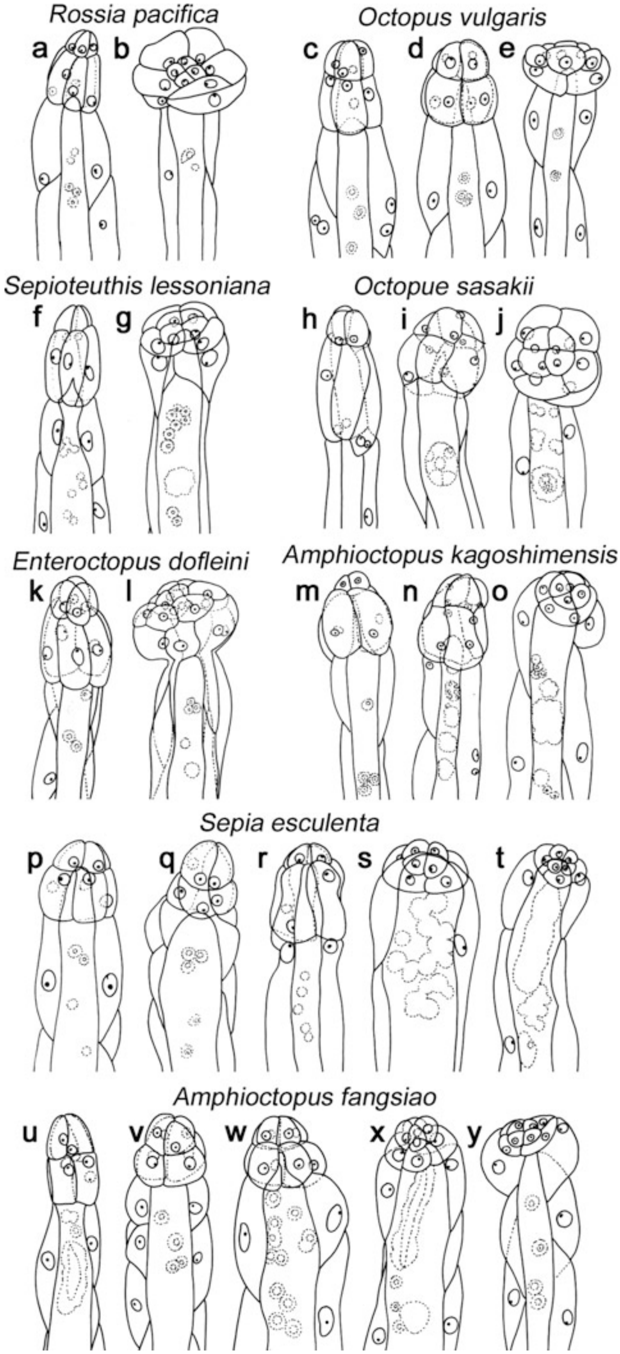

Fig. 15.6 Convergence of the anterior, or attachment, end of dicyemid species. **a** *Dicyema rossiae*; **b** *D. brevicephaloides*; **c** *D. acuticephalum*; **d** *D. misakiense*; **e** *D. japonicum*; **f** *D. koshidai*; **g** *D. orientale*; **h** *D. conodocephalum*; **i** *D. shimantoense*; **j** *D. pileum*; **k** *D. nouveli*; **l** *D. anthinocephalum*; **m** *D. sphaerocephalum*; **n** *D. tosaense*; **o** *D. irinoense*;

References

Aruga J, Odaka YS, Kamiya A, Furuya H (2007) *Dicyema* Pax6 and Zic: tool-kit genes in a highly simplified bilaterian. BMC Evol Biol 7:201

Awata H, Noto T, Endoh H (2005) Differentiation of somatic mitochondria and the structural changes in mtDNA during development of the dicyemid *Dicyema japonicum* (Mesozoa). Mol Gen Genomics 273:441–449

Awata H, Noto T, Endoh H (2006) Peculiar behavior of distinct chromosomal DNA elements during and after development in dicyemid mesozoan *Dicyema japonicum*. Chromosome Res 14:817–830

Bogolepova-Dobrokhotova II (1962) Dicyemidae of the Far-Eastern seas. II. New species of the genus *Dicyemennea*. Zool Zh 41:503–518

Bogolepova-Dobrokhotova II (1963) The current classification of dicyemids. Parazitol Sb 21:259–271

Czaker R (1994) *Kantharella antarctica*, a new and unusual dicyemid mesozoan from the Antarctic. Zool Anz 232:151–158

Czaker R (2000) Extracellular (ECM) components in a very primitive multicellular animal, the dicyemid mesozoan *Katharella antarctica*. Anat Rec 259:52–59

Czaker R (2006) Serotonin immunoreactivity in a highly enigmatic metazoan phylum, the pre-nervous Dicyemida. Cell Tissue Res 326:843–850

Beneden É (1876) Recherches sur les dicyémides, survivants actuels d'un embranchement des mésozoires. Bull Acad R Belg 42:3–111

Furuya H (1999) Fourteen new species of dicyemid mesozoans from six Japanese cephalopods, with comments on host specificity. Species Divers 4:257–319

Furuya H (2005) Three new species of *Dicyema* (Dicyemida; Dicyemidae) from *Octopus kagoshimensis* (Mollusca: Cephalopoda: Octopodidae). Species Divers 10:231–247

Furuya H (2006a) Three new species of dicyemid mesozoans (Phylum Dicyemida) from *Amphioctopus fangsiao* (Mollusca: Cephalopoda), with comments on the occurrence patterns of dicyemids. Zool Sci 23:105–119

Furuya H (2006b) A new species of *Dicyemennea* Whitman, 1883 (Phylum Dicyemida) from *Sepia latimanus* (Mollusca: Cephalopoda: Decapodidae) off Okinawa, Japan. Syst Parasitol 65:205–213

Furuya H (2006c) Two new species of *Dicyema* (Phylum Dicyemida) from *Amphioctopus areolatus* (Mollusca: Cephalopoda: Octopodidae). Species Divers 11:257–269

Furuya H (2007) Redescription of two *Dicyemennea* (Phylum: Dicyemida) from *Rossia pacifica* (Mollusca: Cephalopoda: Decapoda). J Parasitol 93:841–849

Furuya H (2008a) A new dicyemid from *Sepiella japonica* (Mollusca: Cephalopoda: Decapoda). J Parasitol 94:223–229

Furuya H (2008b) Redescription of *Dicyemennea nouveli* (Phylum: Dicyemida) from *Enteroctopus dofleini* (Mollusca: Cephalopoda: Octopoda). J Parasitol 94:1064–1070

Furuya H (2008c) Three new dicyemids from *Octopus sasakii* (Mollusca: Cephalopoda: Octopoda). J Parasitol 94:1071–1081

Fig. 15.6 (continued) **p** *D. minabense*; **q** *D. rhadinum*; **r** *D. mastigoides*; **s** *D. hadrum*; **t** *Pseudicyema nakaoi*; **u** *D. akashiense*; **v** *D. awajiense*; **w** *D. erythrum*; **x** *D. colurum*; **y** *D. helocephalum*. Note calotte shapes were dissimilar as a rule when more than two dicyemid species are present in a single host individual and host species. Calotte shapes in dicyemid species from different host species more closely resemble each other than those of dicyemids observed within the same host species. (See Table 15.1 for generic names of dicyemids)

Furuya H (2009) Two new dicyemids from *Sepia longipes* (Mollusca: Cephalopoda: Decapoda). J Parasitol 95:681–689

Furuya H, Tsuneki K (2003) Biology of dicyemid mesozoan. Zool Sci 20:519–532

Furuya H, Tsuneki K (2005) A new species of dicyemid mesozoan (Dicyemida: Dicyemidae) from *Sepioteuthis lessoniana* (Mollusca: Cephalopoda), with notes on *Dicyema orientale*. Species Divers 10:45–62

Furuya H, Tsuneki K, Koshida Y (1992a) Two new species of the genus *Dicyema* (Mesozoa) from octopuses of Japan with notes on *D. misakiense* and *D. acuticephalum*. Zool Sci 9:423–437

Furuya H, Tsuneki K, Koshida Y (1992b) Development of the infusoriform embryo of *Dicyema japonicum* (Mesozoa: Dicyemidae). Biol Bull 183:248–257

Furuya H, Tsuneki K, Koshida Y (1993) The development of the hermaphroditic gonad in four species of dicyemid mesozoans. Zool Sci 10:455–466

Furuya H, Tsuneki K, Koshida Y (1994) The development of the vermiform embryos of two mesozoans, *Dicyema acuticephalum* and *Dicyema japonicum*. Zool Sci 11:235–246

Furuya H, Tsuneki K, Koshida Y (1997) Fine structure of a dicyemid mesozoan, *Dicyema acuticephalum*, with special reference to cell junctions. J Morphol 231:297–305

Furuya H, Hochberg FG, Tsuneki K (2001) Developmental patterns and cell lineages of vermiform embryos in dicyemid mesozoans. Biol Bull 201:405–416

Furuya H, Hochberg FG, Tsuneki K (2003a) Calotte morphology in the phylum Dicyemida: niche separation and convergence. J Zool 259:361–373

Furuya H, Hochberg FG, Tsuneki K (2003b) Reproductive traits of dicyemids. Mar Biol 142:693–706

Furuya H, Hochberg FG, Tsuneki K (2004a) Cell number and cellular composition in infusoriform larvae of dicyemid mesozoans (Phylum Dicyemida). Zool Sci 21:877–889

Furuya H, Ota M, Kimura R, Tsuneki K (2004b) The renal organs of cephalopods: a habitat for dicyemids and chromidinids. J Morphol 262:629–643

Furuya H, Hochberg FG, Tsuneki K (2007) Cell number and cellular composition in vermiform larvae of dicyemid mesozoans (Phylum Dicyemida). J Zool 272:284–298

Ginetsinskaya TA (1988) Trematodes, their life cycles, biology and evolution. Amerind, New Delhi [translated by Indira Kohli from the original Russian edition published in 1968 by Nauka, Leningrad]

Grell KG (1956) Protozoologie. Springer, Berlin

Hochberg FG (1982) The “kidneys” of cephalopods: a unique habitat for parasites. Malacology 23:121–134

Hochberg FG (1983) The parasite of cephalopods: a review. Mem Natl Mus Victoria 44:109–145

Hochberg FG (1990) Diseases caused by protistans and mesozoans. In: Kinne O (ed) Diseases of marine animals, vol 3. Biologische Anstalt Helgoland, Hamburg, pp 47–202

Hoffman EG (1965) Mesozoa of the sepiolid, *Rossia pacifica* (Berry). J Parasitol 51:313–320

Hyman LH (1940) The invertebrates, vol 1, Protozoa through Ctenophora. McGraw-Hill, New York

Hyman LH (1949) The invertebrates, vol 2, Platyhelminthes and Rhynchocoela. McGraw-Hill, New York

Hyman LH (1956) The invertebrates, vol 5, Smaller coelomate groups. McGraw-Hill, New York

Jereb P, Roper CFE (2005) Cephalopods of the world: an annotated and illustrated catalogue of cephalopod species known to date, vol 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO, Rome

Jereb P, Roper CFE (2010) Cephalopods of the world: an annotated and illustrated catalogue of cephalopod species known to date, vol 2. Myopsid and oegopsid squids. FAO, Rome

Jereb P, Roper CFE, Norman MD, Finn JK (2014) Cephalopods of the world: an annotated and illustrated catalogue of cephalopod species known to date, vol 3. Octopods and vampire squids. FAO, Rome

Katayama T, Wada H, Furuya H, Satoh N, Yamamoto M (1995) Phylogenetic position of the dicyemid Mesozoa inferred from 18S rDNA sequences. Biol Bull 189:81–90

Kobayashi M, Furuya H, Holland WH (1999) Dicyemids are higher animals. Nature (Lond) 401:762

Kozloff EN (1990) Invertebrates. Saunders, Philadelphia

Kubodera T, Lu CC (2002) A review of cephalopod fauna in Chinese–Japanese subtropical region. Natl Sci Mus Monogr 22:159–171

Lapan EA (1975) Studies on the chemistry of the octopus renal system and an observation on the symbiotic relationship of the dicyemid Mesozoa. Comp Biochem Physiol 52:651–657

Lapan EA, Morowitz HJ (1975) The dicyemid Mesozoa as an integrated system for morphogenetic studies. 1. Description, isolation and maintenance. J Exp Zool 193:147–160

Mangold K (1998) The Octopodinae from the eastern Atlantic Ocean and the Mediterranean Sea. Smithson Contrib Zool 586:521–528

McConnaughey BH (1949a) Mesozoa of the family Dicyemidae from California. Univ Calif Publ Zool 55:1–34

McConnaughey BH (1949b) *Dicyemennea nouveli*, a new mesozoan from central California. J Parasitol 45:533–537

McConnaughey BH (1951) The life cycle of the dicyemid Mesozoa. Univ Calif Publ Zool 55:295–336

Norman MD (2000) Cephalopods, a world guide. ConchBooks, Hackenheim

Noto T, Endoh H (2004) A "chimera" theory on the origin of dicyemid mesozoans: evolution driven by frequent lateral gene transfer from host to parasite. Biosystems 73:73–83

Noto T, Yazaki K, Endoh H (2003) Developmentally regulated extra-chromosomal circular DNA formation in the mesozoan *Dicyema japonicum*. Chromosoma 111:359–368

Nouvel H (1947) Les dicyémides, 1re partie: Systématique, générations, vermiformes, infusorigène et sexualité. Arch Biol Paris 58:59–220

Nouvel H, Nakao Y (1938) Dicyémides du Japon. Bull Soc Zool Fr 63:72–80

Ogino K, Tsuneki K, Furuya H (2011) Distinction of cell types in *Dicyema japonicum* (Phylum Dicyemida) by expression patterns of 16 genes. J Parasitol 97:596–601

Okutani T (2005) Cuttlefishes and squids of the world. Seizando-Shoten, Tokyo

Powlowski J, Montoya-Burgos JI, Fahrni JF, West J, Zaninetti L (1996) Origin of the Mesozoa inferred from 18S rRNA gene sequences. Mol Biol Evol 13:1128–1132

Ridley RK (1968) Electron microscopic studies on dicyemid Mesozoa. I Vermiform stages. J Parasitol 54:975–998

Rohde K (1993) Ecology of marine parasites. CAB International, Wallingford

Sasaki M (1929) A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. J Fac Agric Hokkaido Imp Univ 20(suppl):1–338

Smyth JD (1994) Introduction to animal parasitology. Cambridge University Press, Cambridge

Strathmann RR (1990) Why life histories evolve differently in the sea. Am Zool 30:197–207

Strathmann RR, Strathmann MF (1982) The relationship between adult size and brooding in marine invertebrates. Am Nat 119:91–101

Stunkard HW (1954) The life history and systematic relations of the Mesozoa. Q Rev Biol 29:230–244

Stunkard HW (1975) Life-histories and systematics of parasitic flatworms. Syst Zool 24:378–385

Suzuki GT, Tsuneki K, Furuya H (2010) Phylogenetic analysis of dicyemid mesozoans (Phylum Dicyemida) from innexin amino acid sequences—dicyemids are not related to Platyhelminthes. J Parasitol 96:614–625

Chapter 16
Species Diversity of Japanese Ribbon Worms (Nemertea)

Hiroshi Kajihara

Abstract This chapter provides a brief taxonomic conspectus of the Japanese nemerteans with photographs of 100 species. A total of 126 species are recognized in Japanese waters, but there are still at least 77 unreported/undescribed forms awaiting formal description. Previous records of 4 species (*Amphiporus gelatinosus* Coe, 1905; *Cerebratulus longiceps* Coe, 1901; *Cerebratulus montgomeryi* Coe, 1901; and *Emplectonema buergeri* Coe, 1901) are regarded to be unsubstantiated. The names of the 3 species *Cerebratulus penniger* Iwata, 1957, *Euborlasia proteres* Iwata, 1957, and *Lineus nipponensis* Senz, 2001 are treated as *nomina dubia*. The following 6 are herein judged as junior synonyms of older names: *Amphiporus insolitus* Iwata, 1954 [=*Diplomma serpentina* (Stimpson, 1855)]; *Amphiporus reduncus* Iwata, 1957 and *Amphiporus retrotumidus* Iwata, 1957 [=*Nipponnemertes ogumai* (Yamaoka, 1947)]; *Cerebratulus albocirculus* Iwata, 1957 [=*Lineus albovittatus* (Stimpson, 1855)]; *Cerebratulus fasciatus* Stimpson, 1857 [=*Notospermus geniculatus* (Delle Chiaje, 1828)]; and *Tetrastemma yamaokai* Iwata, 1954 [=*Tetrastemma roseocephalum* (Yamaoka, 1947)]. Five species are herein added as new members of the Japanese nemertean fauna: *Cerebratulus rubellus* (Stimpson, 1855); *Cerebratulus signatus* Coe, 1905; *Micrura callima* Sundberg and Gibson, 1995; *Tetrastemma pimaculatum* Chernyshev, 1998; and *Tortus tokmakovae* Chernyshev, 1991.

Keywords Pacific • Sea of Japan • Sea of Okhotsk • East China Sea • Marine invertebrates • Taxonomy • Systematics • Biogeography

16.1 Introduction

Ribbon worms (phylum Nemertea) are mostly marine, benthic, carnivorous invertebrates feeding on small crustaceans, polychaetes, and mollusks (McDermott and Roe 1985), with about 1300 species known worldwide (Kajihara et al. 2008). The phylum consists of three major groups: Palaeonemertea, Pilidiophora, and

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Hoplonemertea. Although it is likely that Pilidiophora and Hoplonemertea comprise a clade (=Neonemertea), whether Palaeonemertea is monophyletic could not be determined by available data based on standard Sanger sequencing (Thollesson and Norenburg 2003; Andrade et al. 2012). Recent transcriptome-based phylogenomic analysis suggests monophyly of Palaeonemertea (Andrade et al. 2014), although it lacked such important palaeonemertean taxa as *Carinina* and *Callinera*.

A literature-based taxonomic catalogue of Japanese nemerteans listed 120+ species as valid (Kajihara 2007). Since then, 11 species have been either newly established from Japan or added to the known Japanese nemertean fauna (Kajihara and Fujita 2008; Kajihara and Ise 2008; Kajihara and Lindsay 2010; Kajihara et al. 2011a, b, 2012, 2015, 2016; Kajihara and Kuris 2013; Kajihara and Nishi 2013; Kajihara 2015). In this chapter, all the known species are briefly annotated with comments on distribution and, when applicable, taxonomic issue. Photographs are provided for as many species as possible to facilitate identification for non-experts.

16.2 Palaeonemertea

Of the 12 species of palaeonemerteans known in Japanese waters, *Cephalothrix simula* (Iwata, 1952) and *Tubulanus punctatus* (Takakura, 1898) are the most common and widely distributed in this area; the rest of the species are poorly studied.

16.2.1 Cephalotrichidae

Cephalothrix simula (Fig. 16.1a, b) dwells intertidally among algal holdfasts or under stones. It has been found in the Sea of Okhotsk, the Sea of Japan, the northern part of the Yellow Sea, and the Pacific Coast along Hokkaido and Honshu, Japan (Kajihara et al. 2013). In addition, distribution along the Mediterranean and the Atlantic Coasts in European waters (Chen et al. 2010; Fernández-Álvarez and Machordom 2013), as well as the Pacific Coasts in North America (Fernández-Álvarez and Machordom 2013), has been molecularly confirmed, suggesting an artificial introduction from the Northeast Pacific. The species accumulates high concentration of tetrodotoxin (TTX, the puffer-fish toxin) and its derivatives, with the highest toxicity per a single worm exceeding the human lethal dose (Asakawa et al. 2013).

In Kyushu and southward, *Cephalothrix fasciculus* (Iwata, 1952) (Fig. 16.1c, d) is distributed, with its southern range extending into Vietnamese waters (A.V. Chernyshev, personal communication). In this area, cephalotrichids having a yellowish body with reddish tip of head co-occur; these include *C. simula* and *C. fasciculus*, and possibly *C. hongkongiensis* Sundberg et al., 2003. Because they

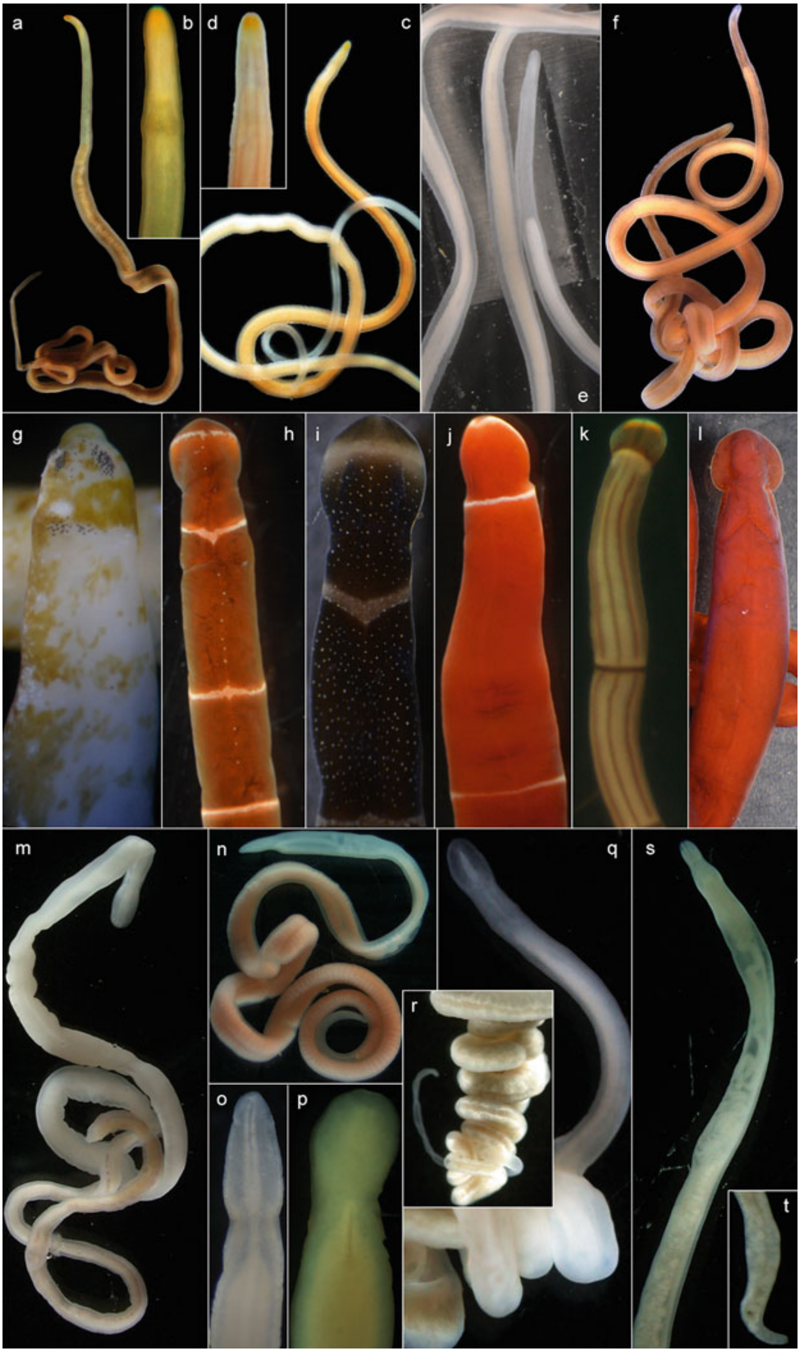

Fig. 16.1 **a, b** *Cephalothrix simula* (**a**, entire animal; **b**, magnification of head), subtidal, among cultured oysters, Hiroshima Bay. (©Japanese Society of Zoology.) **c**, **d** *Cephalothrix fasciculus* (**c**, entire animal; **d**, magnification of head), intertidal, Fukue. (©Japanese Society of Zoology.) **e** '*Procephalothrix filiformis*' sensu Iwata (1954a), intertidal, Akkeshi Bay. **f** *Cephalothrix* sp.,

look similar to each other, molecular inspection is necessary for reliable identification.

Uniformly pale-coloured cephalotrichids are found in Hokkaido; they seem to be composed of at least two morphospecies (Fig. 16.1e, f). However, application of names to those forms requires further taxonomic scrutiny, although *Cephalothrix notabilis* Iwata, 1954 is one candidate. Two unidentified species, each in *Cephalotrichella* and *Balionemertes* (Fig. 16.1g), were obtained in Hokkaido and Okinawa, respectively (Kajihara, unpublished data).

16.2.2 Tubulanidae s.l.

Tubulanus punctatus (Fig. 16.1h) is found not only from the intertidal zone, but also subtidally down to 115 m depth (off Nagato, Yamaguchi Prefecture, the Sea of Japan); the maximum intraspecific variation in 578 nt of the cytochrome *c* oxidase subunit I (COI) gene in terms of uncorrected *p*-distance among the Japanese populations so far observed is 6.2 % between individuals from Akkeshi Bay and Hiroshima Bay. From Misaki (the type locality of *T. punctatus*), a form having a similar but slightly different body marking has been found (Fig. 16.1i); molecular data should confirm its identity.

Tubulanus roretzi Senz, 1997 was described based on fixed material. Neither the coloration in the living state nor the exact locality of the species is known (Senz 1997). *Tubulanus roretzi* was established by anatomical states alleged to be different from other congeners, but they actually are found in some species, including *T. punctatus*. That is, *T. roretzi* may not be distinguishable from *T. punctatus* solely by the internal morphology, and is thus likely to be synonymous with *T. punctatus*.

There are at least four, less common congeners in Japanese waters, including *T. ezoensis* Yamaoka, 1940 (Fig. 16.1j), *T. capistratus* Coe, 1904, *T. tamias* Kajihara et al., 2015 (Fig. 16.1k), and a dark-orange, uniformly coloured form (Fig. 16.1l), which resembles *Carinella rubra* Griffin, 1898 and *Carinella speciosa* Coe, 1901; the latter two were described from the Pacific Coast of North America, and were synonymized with the European form *Tubulanus polymorphus* Renier, 1804 by Coe (1940), which might warrant reconsideration. *Tubulanus capistratus* is

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Fig. 16.1 (continued) intertidal, Oshoro. **g** *Balionemertes* sp., Nansei Islands. (Photograph by K. Kakui.) **h** *Tubulanus punctatus*, intertidal, Oshoro. **i** *Tubulanus* cf. *punctatus*, Misaki. (Photograph by S. Tomioka.) **j** *Tubulanus ezoensis*, intertidal, Akkeshi. **k** *Tubulanus tamias*, subtidal (10 m depth), Tomioka Bay. **l** *Tubulanus* sp., subtidal (90 m depth), Sagami Bay. **m** *Carinina plecta*, intertidal, Hamanako. **n** *Carinoma hamanako*, intertidal, Hamanako. **o** Tubulanidae sp., subtidal (90 m depth), Sagami Bay. **p** Tubulanidae sp. subtidal (500 m depth), off Toimisaki Cape. **q**, **r** *Hubrechtella ijimai* (**q**, anterior body; **r**, tail), intertidal, Hamanako. (©Magnolia Press.) **s**, **t** *Hubrechtella kimuraorum* (**s**, anterior body; **t**, tail) (**a**–**d** Reproduced from Kajihara et al. 2013; **q**, **r** reproduced from Kajihara 2006) similar to *T. punctatus* in appearance by having a reddish-brown basement body colour with white bands and stripes, but it has a more definite mid-dorsal stripe.

Four species of named—*Callinera nishikawai* Kajihara, 2006; *Carinesta uchidai* Iwata, 1952; *Carinina plecta* Kajihara 2006 (Fig. 16.1m); *Carinoma hamanako* Kajihara et al., 2011b (Fig. 16.1n)—and a few unnamed (Fig. 16.1o, p), uniformly whitish palaeonemerteans have been found both intertidally and subtidally along the Pacific Coast in Honshu and the Nansei Islands (Kajihara, personal observation).

16.3 Pilidiophora

16.3.1 Hubrechtellidae

Hubrechtella ijimai (Takakura, 1922) (Fig. 16.1q, r), *H. kimuraorum* Kajihara, 2006 (Fig. 16.1s, t), *Tetramys ramicerebrum* Iwata, 1957, and '*Tubulanus*' *lucidus* Iwata, 1952 are the named hubrechtellids reported from Japan. The monotypic genus *Tetramys* Iwata, 1957 is almost certainly a junior synonym of *Hubrechtella*; it is alleged to be different from *Hubrechtella* by the presence of the body wall inner longitudinal and inner circular muscle layers, which, however, appear to be a misinterpretation of the character state, judging from one of the figures in the original description (Iwata 1957, pl. II., fig. 5). '*Tubulanus*' *lucidus* shows characteristics that are common in *Hubrechtella*, viz., the mid-dorsal blood vessel and the cerebral sensory organs submerged in the blood lacuna; these characters are never found in *Tubulanus*. Undetermined hubrechtellids (Kajihara, unpublished data) have been found subtidally in Tomioka Bay (10 m depth).

16.3.2 Valenciniidae

Eight species of *Baseodiscus* have been recorded from Japan: *B. curtus* (Hubrecht, 1879) (Fig. 16.2a), *B. delineatus* (Delle Chiaje, 1825) (Fig. 16.2b), *B. hemprichii* (Ehrenberg, 1831) (Fig. 16.2c), *B. mexicanus* (Bürger, 1893) (Fig. 16.2d), *B. nipponicus* (Hubrecht, 1887), *B. princeps* (Coe, 1901) (Fig. 16.2e), *B. quinquelineatus* (Quoy and Gaimard, 1833) (Fig. 16.2f), and *B. takakurai* Gibson, 1995 (Fig. 16.2g). Three undescribed congeners have been confirmed and are awaiting formal description (Kajihara, unpublished data).

Cephalomastax brevis Iwata, 1957, the sole member of the monotypic genus *Cephalomastax*, is known only from the type material from Sagami Bay. Two specimens of putative *C. brevis* were recently collected in Sagami Bay (Fig. 16.2h).

A total of three or more undetermined species of heteronemerteans without cephalic slits, probably representing valenciniids and paralineids, have been

Fig. 16.2 **a** *Baseodiscus curtus*, subtidal, among cultured oysters, Hiroshima Bay. **b** *Baseodiscus delineatus*, intertidal, Misaki. **c** *Baseodiscus hemprichii*, Nansei Islands. (Photograph by K. Kakui.) **d** *Baseodiscus mexicanus*, Manza (Okinawa), subtidal (3–4 m depth). (Photograph by R. Yoshida.) **e** *Baseodiscus princeps*, intertidal, Akkeshi. **f** *Baseodiscus quinquelineatus*,

collected subtidally in Sagami Bay (Fig. 16.2i) and Tomioka Bay (Fig. 16.2j); these are uniformly white or pinkish in colour, with the intestine often being reddish. These forms are important for elucidating the basal topology of the pilidiophoran phylogenetic tree.

16.3.3 Paralineidae

Paralineopsis taki Iwata, 1993, a monospecific genus, is 20 cm long and 1 mm wide; it is anteriorly white, with alimentary canal tinged with pale yellow or flesh colour, lacking obvious horizontal lateral cephalic slits. The species is important for pilidiophoran phylogeny but has been known only by a single specimen from Onomichi.

16.3.4 Schizonemertini

Forty-nine species of heteronemerteans with horizontal lateral cephalic slits have been reported from Japanese waters, of which 14 are known only from original descriptions. There are at least 13 potentially undescribed forms (Kajihara, unpublished data). The genus-level taxonomy does not reflect phylogeny (Schwartz 2009; Andrade et al. 2012; Kvist et al. 2014); many species currently classified in *Cerebratulus*, *Lineus*, and *Micrura* may be transferred to different genera. For this purpose, as many species as possible should be placed in a molecular phylogenetic context in future studies.

Cerebratulus albocirculus Iwata, 1957 is only known by the holotype in the preserved state, which is 16 cm long and 6 mm wide, collected subtidally (10 m depth) in Sagami Bay. The head is dark green, with a white transverse ring; the body is yellowish green. It is herein synonymized with *Lineus albovittatus* (Stimpson, 1855), which is to be transferred to *Notospermus* (Chernyshev 2016).

Fig. 16.2 (continued) Irabujima. (Photograph by R. Yoshida.) **g** *Baseodiscus takakurai*, subtidal (10 m depth), Koajiro Bay. (Photograph by H. Kohtsuka.) **h** *Cephalomastax brevis*, subtidal (250–300 m depth), Sagami Bay. **i** Valenciniidae sp., subtidal (90 m depth), Sagami Bay. **j** Valenciniidae sp., subtidal (10 m depth), Tomioka Bay. **k** *Cerebratulus carnosus*, intertidal, Misaki. (Photograph by Y. Ise.). **l** *Cerebratulus communis*, intertidal, Hamanako. **m** cf. *Cerebratulus formosus*, subtidal (90 m depth), Sagami Bay. **n** *Cerebratulus fuscus* sensu Takakura (1898), subtidal, among cultured oysters, Hiroshima Bay. **o** cf. *Cerebratulus macroren*, subtidal (200 m depth), Sagami Bay. **p** *Cerebratulus marginatus* auct., intertidal, Akkeshi. **q** '*Cerebratulus*' *rubellus*, Okinawa. **r** *Cerebratulus signatus*, subtidal (200 m depth), off Iwate Prefecture. (Photograph by K. Kakui). **s** cf. *Cerebratulus superniger*, subtidal (200 m depth), Sagami Bay. **t** *Euborlasia nigrocincta*, subtidal (SCUBA), Izu. **u** *Gorgonorhynchus albocinctus*, subtidal (SCUBA), Taketomi Island. (Photograph by S. Tomioka.) (**u** Reproduced from Kajihara 2015)

Cerebratulus carnosus Takakura, 1898 (Fig. 16.2k) is a large species (>30 cm in length). The head is whitish; in contrast with *C. communis*, its anterior is rounded and slightly wider than the succeeding portion. The neck is white. The body is posteriorly orange, then further back reddish brown. The species is only known from the type locality, Misaki.

Cerebratulus communis Takakura, 1898 is a problematic taxon. In contrast to *C. carnosus*, the head is sharply pointed. Takakura (1898) recognized two colour variations: (1) tip of head white, head flesh colour, body dark green; and (2) head whitish, body flesh colour. Apart from the type locality (Misaki), similar forms have been collected in Otsuchi Bay (60–100 m depth); Hamanako (intertidal, Fig. 16.2l); and Seto Inland Sea (30 m depth) (Kajihara, unpublished data). A DNA taxonomy approach is necessary for species delimitation among other uniformly whitish or pinkish cerebratulids such as *Cerebratulus macroren* Hubrecht, 1887, *Micrura akkeshiensis* Yamaoka, 1940, and '*Micrura alaskensis*' Coe, 1901, to which a complex of five different cryptic species could be attributed on the Pacific Coast of USA, of which one was also found in the Sea of Okhotsk (Hiebert and Maslakova 2015).

Cerebratulus fasciatus Stimpson, 1857 is only known by the original description based on material obtained sublittorally from a bottom of muddy sand at a depth of about 7.4 m in Hokkaido. The body is a purple-brown colour, with white rings arranged at intervals. It is herein synonymized with *Notospermus geniculatus*; the latter, however, forms a species complex (M. Schwartz, personal communication).

Cerebratulus formosus Iwata, 1957 is common in bottoms near Misaki (10–100 m depth). The body is pale creamy white, covered with brown mottles (Fig. 16.2m).

Cerebratulus fuscus sensu Takakura (1898) was collected from several fathoms off Jôgashima. It might represent *Eousia verticivaria* Gibson, 1990 or related species. Similar forms have been collected off Jôgashima (100–300 m depth; H. Kohtsuka, personal communication), Hiroshima Bay (Fig. 16.2n), Tomioka Bay (Kajihara, personal communication), and Okinawa (M. Schwartz, personal communication).

Cerebratulus longiceps Coe, 1901 was recorded by Coe (1944) from 250 m depth, off Izu-Ôshima, which is under an oceanic environment quite different from that in Yakutat, AK (USA), the type locality of the species. *Cerebratulus longiceps* is externally indistinguishable from *Lineus alborostratus* Takakura, 1898. Coe's (1944) record cannot be substantiated.

Cerebratulus macroren Hubrecht, 1887 lacks colour markings, as originally collected from a depth of 640 m in Sagami Bay. Pale-coloured, white or pink fragments of heteronemerteans are frequently found among dredged material from Sagami Bay (Fig. 16.2o); they might be referable to *C. macroren*.

Cerebratulus marginatus auct. non Renier, 1804 is found in many places in Japan, both intertidally and subtidally (Fig. 16.2p). The Japanese form(s) referred to by this name is different from *C. marginatus* s. str. from Naples (Schwartz 2009).

Cerebratulus montgomeryi Coe, 1901 was recorded from Japanese waters by Coe (1944) based on material from 600 m depth, off Hokkaido; it is outside the range of the known habitat of the species. Coe's (1944) record cannot be substantiated.

Cerebratulus nigrofuscus Stimpson, 1857 is only known by the original description. The body is 14 cm long, 2 mm wide, dorsally blackish dark red. The head is anteriorly truncated, the succeeding region is half that of the neck in width. The mouth is elongated. Intertidal between stones in Amami Ōshima.

Cerebratulus penniger Iwata, 1957 is only known by the holotype obtained from a depth of 380 m in Sagami Bay. It had been preserved in Bouin's fluid; thus the exact body colour in life is not known, but it was probably pale coloured, having no markings. The species is allegedly "easily distinguishable in the external features of the body" (Iwata 1957), with the lateral edges of the body being flattened and protruded laterally like a narrow longitudinal fin. It would be either an artefact during fixation or, less likely, indicative that the species may belong to *Diplopleura*. The name is herein regarded as *nomen dubium*.

Cerebratulus rubellus (Stimpson, 1855) was originally described from Hong Kong. It is also distributed in Okinawa (Nakijin and Motobu; M. Schwartz, unpublished data) (Fig. 16.2q); herein added as a new member of the Japanese nemertean fauna.

Cerebratulus signatus Coe, 1905 was originally described from the Bering Sea (110 m depth). In Peter the Great Bay, the species can be found among stomach contents in a few species of flounders (Chernyshev 2014). A couple of specimens from a depth of 200 m off Iwate Prefecture (Fig. 16.2r; K. Kakui, personal communication) constitute the first record of this species from Japanese waters.

Cerebratulus subacutus (Stimpson, 1857) is described from muddy sediment in Naha, Okinawa. The body is 9 cm long, 3 mm wide, anteriorly flesh coloured, posteriorly blood brown; the tail is rounded. A reddish heteronemertean is often found in a mud flat in Katsuren, Okinawa (R. Yoshida, personal communication), which may be referable to *C. subacutus*.

Cerebratulus superniger Iwata, 1957 is dorsally dark brown, ventrally pale yellowish brown. The holotype, 20 cm long and 6 mm wide, was collected from a depth of 10 m in Sagami Bay. Fragments of heteronemerteans with similar colouration, although smaller in size, that were collected from about 200 m depth in Sagami Bay may be referable to *C. superniger* (Fig. 16.2s).

Cerebratulus zebra Punnett and Cooper, 1909 was originally described from Sri Lanka. Fragments of the intestinal region (whitish with dark brown rings), from 410 m in Sagami Bay, were identified and reported by Iwata (1957).

Diplopleura japonica Stimpson, 1857 is an enigmatic species, only known by the original description. The body, about 4 cm long and 3 mm wide, is a honey yellow colour, with its lateral edges being dorsally folded, a character that is unique for the genus among the phylum.

Euborlasia gotoensis Iwata, 1952 is 10 cm long, 3 to 10 mm wide, anteriorly white, posteriorly becoming dull brown or reddish brown, with a pointed head. The rhynchocoel appears as a dark-coloured stripe. Reported from Fukue and Sado.

Euborlasia nigrocincta Coe, 1940 has a characteristic body colouration (Fig. 16.2t) and appears to be distributed along the Pacific Rim; from Japanese waters, it has been recorded from Ito (Shizuoka) and Namerikawa (Toyama) (Kajihara and Nishi 2013).

Euborlasia proteres Iwata, 1957 was described based on a preserved specimen fixed in Bouin's fluid; thus the body coloration in life, if any, is unknown. It is regarded as a *nomen dubium*.

Gorgonorhynchus albocinctus Kajihara, 2015 (Fig. 16.2u) has a branched proboscis; it is only known by the holotype from Taketomi Island.

Hinumanemertes kikuchii Iwata, 1970 is a brackish-water species so far only known from Lake Hinuma. The body, 12 cm long and 1 mm width when extended, is light yellowish brown, and the intestine is tinged with a dull orange colour; a short caudal cirrus is present.

Iwatanemertes piperata (Stimpson, 1855) is commonly found in warmer waters (Fig. 16.3a); the northern limit of the distribution in Japanese waters appears to be Sado in the Sea of Japan and Misaki along the Pacific. It can be distinguished from the similar form, *Lineus mcintoshii* (Langerhans, 1880) (Fig. 16.3b), in that the former has a pair of orange stripes laterally on both sides, whereas the latter has a mid-dorsal orange stripe.

Lineopselloides albilineus Gibson, 1990 (Fig. 16.3c) inhabits the intertidal zone and shallow waters along the Pacific Coast of Honshu and the Seto Inland Sea. It is similar to *Lineus bilineatus* Renier, 1804, both possessing a brownish body with a white mid-dorsal stripe (Fig. 16.3d–f). However, they differ in colouration of the head. In *Lineopselloides albilineus*, the anterior edge of the head is not bordered with a white colour, and the mid-dorsal stripe is composed of a single line. In *Lineus bilineatus*, the anterior edge of the head is whitish; the mid-dorsal stripe is composed of two white lines with a translucent area between; the anterior portion of the stripe may become wider (Fig. 16.3e). *Lineus bilineatus* sensu Iwata (1954) (Fig. 16.3f) has black eyes and probably represents a different species. A DNA taxonomy approach is necessary to delineate the species, especially if those '*Lineus bilineatus*' in Japanese waters are conspecific with the European form.

Lineus alborostratus Takakura, 1898 (Fig. 16.3g) is one of the most common heteronemerteans in Japanese waters, recorded from Hokkaido to the Seto Inland Sea; it has also been recorded from Peter the Great Bay, the South Kuril Islands, South Sakhalin, and the Yellow Sea (summarized by Chernyshev 2014). The body is variously brownish to purplish, with the tip of the head bordered by a white band.

Lineus albovittatus (Stimpson, 1855) is closely related to *Notospermus geniculatus* but differs from the latter by the anteriormost white band being straight (instead of medially an inversed V-shape as in *N. geniculatus*) and lacking the white rings that are arranged more or less regularly throughout the body in *N. geniculatus* [*L. albovittatus* is to be transferred to *Notospermus* (Chernyshev 2016)]. *Lineus hancocki* Punnett and Cooper, 1909 and/or *L. indicus* Punnett and Cooper, 1909 might be conspecific with *L. albovittatus*. '*Lineus albovittatus*' sensu Iwata (1954b), ventrally white in colour, is a different taxon. On Tanegashima Island, a 'hybrid' morphotype between *L. albovittatus* and *N. geniculatus* was found, in which the anteriormost transverse white line on the dorsal side of the head is straight and numerous white rings are present on the body.

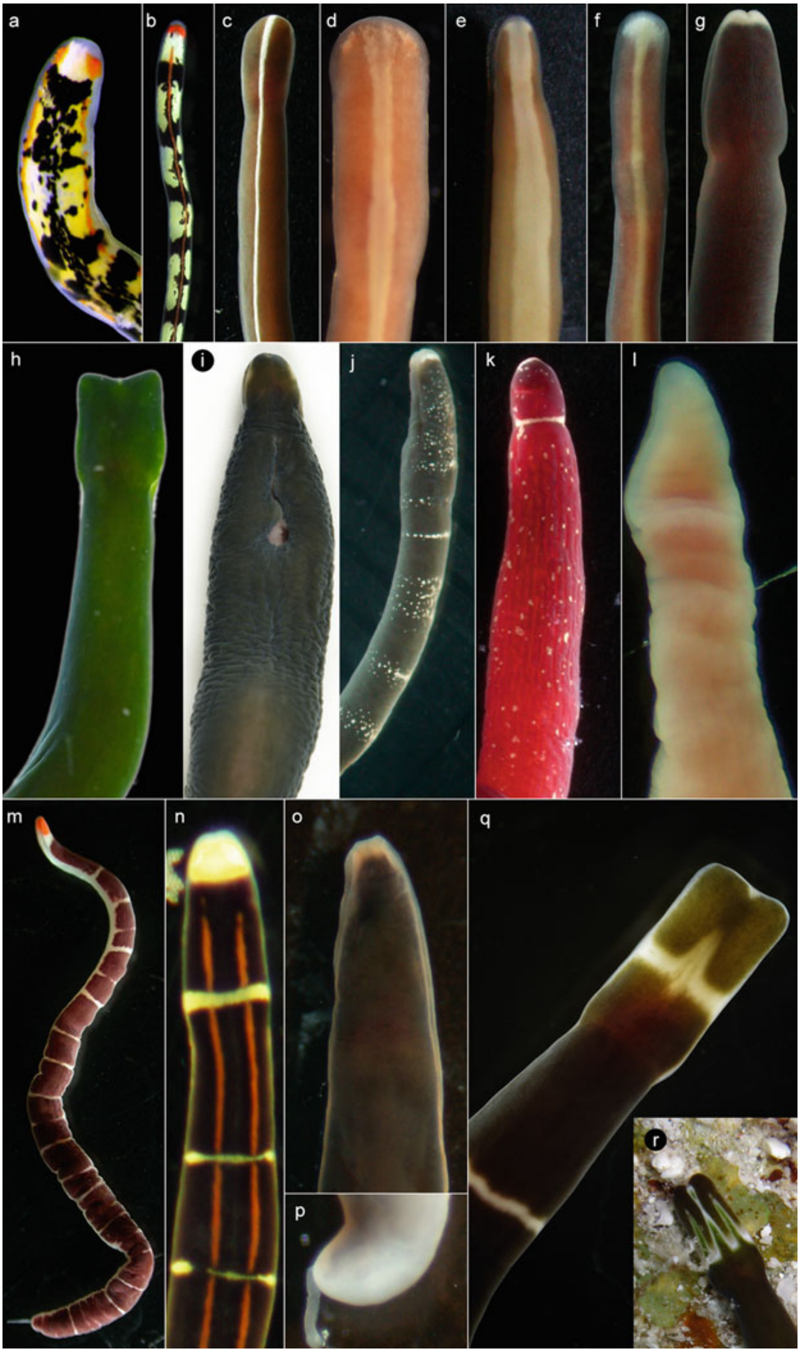

Fig. 16.3 **a** *Iwatanemertes piperata*, intertidal, Misaki. (Photograph by H. Kohtsuka). **b** *Lineus mcintoshii*, intertidal, Fukue. **c** *Lineopselloides albilineus*, intertidal, Hamanako. **d** cf. *Lineus bilineatus*, subtidal (200 m depth), Sagami Bay. **e** cf. *Lineus bilineatus*, intertidal, Fukue. **f** '*Lineus bilineatus*' sensu Iwata (1954a), Akkeshi. **g** *Lineus alborostratus*, intertidal, Akkeshi. **h** *Lineus fuscoviridis*,

Lineus bipunctatus Takakura, 1898 has a translucent, pale yellow body, 2 cm long and 0.5 mm wide. There is a crescent-shaped white cephalic patch on the dorsal surface of the tip of the head, on which a pair of small red dots are present. The species is known only by the original description based on material from among hydroids collected from depths of 3.7 to 5.5 m near Jôgashima.

Lineus cancelli Iwata, 1954, about 6 cm long and 3 mm wide, was described from material collected intertidally under stones in Shirahama. The body is dull yellow, with numerous dark brown transverse markings irregularly arranged on the dorsal surface. It is only known by the original description.

Lineus caputornatus Takakura, 1898 is 5 cm in length and 1 mm in width; the dorsal surface of the body is anteriorly blackish brown, posteriorly reddish brown, ventrally paler. The dorsal surface of the head is anteriorly colourless. A yellow cephalic patch is present on the colourless area, the anterior and posterior edges of which are surrounded by reddish-brown dots arranged in a crescent-shaped row. The species is known only by the original description based on material from among hydroids collected at depths of 3.7 to 5.5 m in Jôgashima.

Lineus fulvus Iwata, 1954 is known from a single specimen collected from among laminarian holdfasts in Rishiri Island. The body is anteriorly brownish yellow, and posteriorly yellow; with a white band on tip of head. Eyes, which can be found in cross sections, are present along the anterolateral margin of the head.

Lineus fuscoviridis Takakura, 1898 (Fig. 16.3h) has a uniformly green body. It is very common in warmer waters around Japan, with Niigata and Chiba Prefectures being the northernmost distribution range; the species also has been recorded from the Yellow Sea (Chernyshev 2014).

Lineus grubei sensu Takakura (1898) is 6 cm long, 1 mm wide, uniformly dark brown tinged with a purple colour, ventrally paler. There is a yellowish-white transverse line on the dorsal surface near the tip of the head; anterior to this line are two or three dots with the same colour as the line.

'*Lineus longifissus*' sensu Takakura (1898) (Fig. 16.3i) is rarely found in intertidal muddy sand flats along the Pacific Coast of Honshu from Misaki and southward.

Lineus mcintoshii (Langerhans, 1880) (Fig. 16.3b) is a rare species. From Japan, it has been found in Misaki (Takakura 1898) and Fukue (Kajihara, personal observation). It is distributed in warmer waters in the Indo-West Pacific region, so far recorded from Madeira (Langerhans 1880); Kerala, India (Shynu et al. 2015); and the South China Sea (Chernyshev 2015).

Fig. 16.3 (continued) intertidal, Misaki. **i** '*Lineus longifissus*' sensu Takakura (1898), intertidal, Misaki. **j** *Lineus subcingulatus*, intertidal, Shimoda. **k** *Lineus torquatus*, intertidal, Akkeshi. **l** '*Micrura alaskensis*' sensu Yamaoka (1940), intertidal, Akkeshi. **m** *Micrura bella*, intertidal, Oshoro. **n** *Micrura callima*, Motobu. **o**, **p** '*Micrura japonica*', intertidal, Okinawa (**o**, head; **p**, tail). **q** *Notospermus geniculatus*, intertidal, Misaki. **r** *Notospermus tricuspidatus*, Kerama Islands. (Photograph by A. Ono)

Lineus nigrofuscus (Stimpson, 1857) is only known from the original description. The body is 14 cm long and 2 mm wide, dorsally blackish dark red. The head is elongated and continuous with the body. The frontal edge of the head is truncated, the width of which is half that of the neck. Intertidal between stones in Amami Ōshima.

Lineus nipponensis Senz, 2001 was described based on a preserved specimen, which is up to 10 cm long, 3.6 mm wide, and uniformly yellowish white in colour. The exact habitat and locality are not recorded. One will never be able to assign with certainty any material to this species in the future, and the name is herein regarded as *nomen dubium*.

Lineus spatiosus Iwata, 1954 was described based on a single specimen collected intertidally under a stone in Akkeshi. The body is 40 cm long and 1 cm wide, uniformly reddish purple in colour. The anterior and lateral edges of the head are white. About 25 small, ocelli-like spots are arranged on the upper surface of lateral cephalic slits.

Lineus subcingulatus Takakura, 1898 was described based on material among hydroids collected from depths of 3.7 to 5.5 m near Jôgashima. It was also collected among the holdfasts of the brown algae *Eisenia bicyclis* in Shimoda (Kajihara, personal observation) (Fig. 16.3j).

Lineus torquatus Coe, 1901(Fig. 16.3k) is abundant in Akkeshi. Coe (1901) recognized 'brown' and 'cherry' colour morphs, which represent different species (Manchenko and Kulikova 1996). Both morphs occur in Akkeshi, but the 'cherry' morph is more common (Yamaoka 1940; Kajihara, personal observation).

'*Micrura alaskensis*' sensu Yamaoka (1940) (Fig. 16.3l) and *M. akkeshiensis* Yamaoka, 1940 from Akkeshi are supposed to be distinguishable by the neck (constricted in *M. alaskensis* versus not constricted in *M. akkeshiensis*), a mid-ventral flesh-coloured stripe (present in *M. alaskensis* versus absent in *M. akkeshiensis*), and the caudal cirrus (long in *M. alaskensis* versus short in *M. akkeshiensis*) (Yamaoka 1940); further taxonomic scrutiny is necessary with regard to these two forms (cf. Hiebert and Maslakova 2015).

Micrura bella (Stimpson, 1857) (Fig. 16.3m) is common from middle Honshu to Hokkaido. It is also distributed in Peter the Great Bay, the South Kuril Islands, South Sakhalin, and the Yellow Sea (summarized by Chernyshev 2014).

Micrura callima Sundberg and Gibson, 1995 is distributed in Australia (Sundberg and Gibson 1995) and Vietnam (Chernyshev 2011). The species is herein added as a new member of the Japanese nemertean fauna; it is common in Okinawa (Fig. 16.3n).

Micrura dorsovittata Takakura, 1898 is only known from a single specimen collected near Jôgashima. The body is 1.5 cm long, 0.5 mm wide, translucent; dark purple rectangles are arranged dorsally. Eyes are present.

'*Micrura japonica*' Iwata, 1952 (Fig. 16.3o, p) is likely to be a junior synonym of *Micrura formosana* Yamaoka, 1939 and *Meckelia nigra* Stimpson, 1855 (Kajihara, personal observation). Common in warmer waters, its northerly distribution reaching Sado Island (Niigata) and Sagami Bay.

Micrura magna Yamaoka, 1940 was described from a single individual found under a stone in Daikokujima Island, Hokkaido; it was also found in Peter the Great Bay (Chernyshev 2014). The body is up to 60 cm long, pale yellowish green in colour, with dark brown spots irregularly arranged in the posterior two thirds, anteriorly gradually becoming dark brown; the head and the neck are dark brown; a caudal cirrus is present.

Micrura multinotara Iwata, 1957 was described from a preserved specimen obtained subtidally at depths of 30 to 40 m in Sagami Bay (Ogashima). It has a pale-coloured body, dorsally with numerous brown transverse bands.

Nipponomicrura uchidai (Yamaoka, 1940) was described from Muroran. It has also been reported from Peter the Great Bay (Chernyshev 2008). Its body is purple, with a white band at the posterior end of the lateral cephalic slits; caudal cirrus present.

Notospermus geniculatus (Delle Chiaje, 1828) (Fig. 16.3o) is a common species in warmer waters worldwide. It has been found subtidally near Shakotan, Hokkaido, probably the northernmost range in Japanese waters (Kajihara, personal observation).

Notospermus tricuspidatus (Quoy and Gaimard, 1833) (Fig. 16.3q) is also a common species in warmer waters in the Indo-Pacific. Not listed in Kajihara (2007), but the species has recently been added to the Japanese nemertean fauna, so far recorded in Yakushima Island (Kajihara et al. 2016), Okinawa Island (Kajihara et al. 2016), and the Kerama Islands (A. Ono, personal communication).

Ramphogordius sanguineus (Rathke, 1799) (Fig. 16.4a) has previously been recorded as ‘*Lineus gesserensis*’ and ‘*Lineus vegetus*’ from Japanese waters. It shows a circumglobal distribution in the temperate intertidal zones of the Northern Hemisphere (Kang et al. 2015). The ability of asexual reproduction causes propagation on a massive scale in such a limited condition as an aquarium tank. Kajihara and Fujita (2008) reported such an incidence of explosive multiplication observed in an exhibition tank for the Japanese horseshoe crab *Tachypleus tridentatus* (Leach, 1819), where 135 individuals were collected from 500 ml of sand, which is equivalent to 13,500 individuals per square metre if the worms dwelt in the upper 5-cm layer.

Uchidana parasita Iwata, 1967 is only known by the original description. It is parasitic on the bivalve *Mactra chinensis* Philippi, 1846; gill tissues under the process of digestion were found in the intestine.

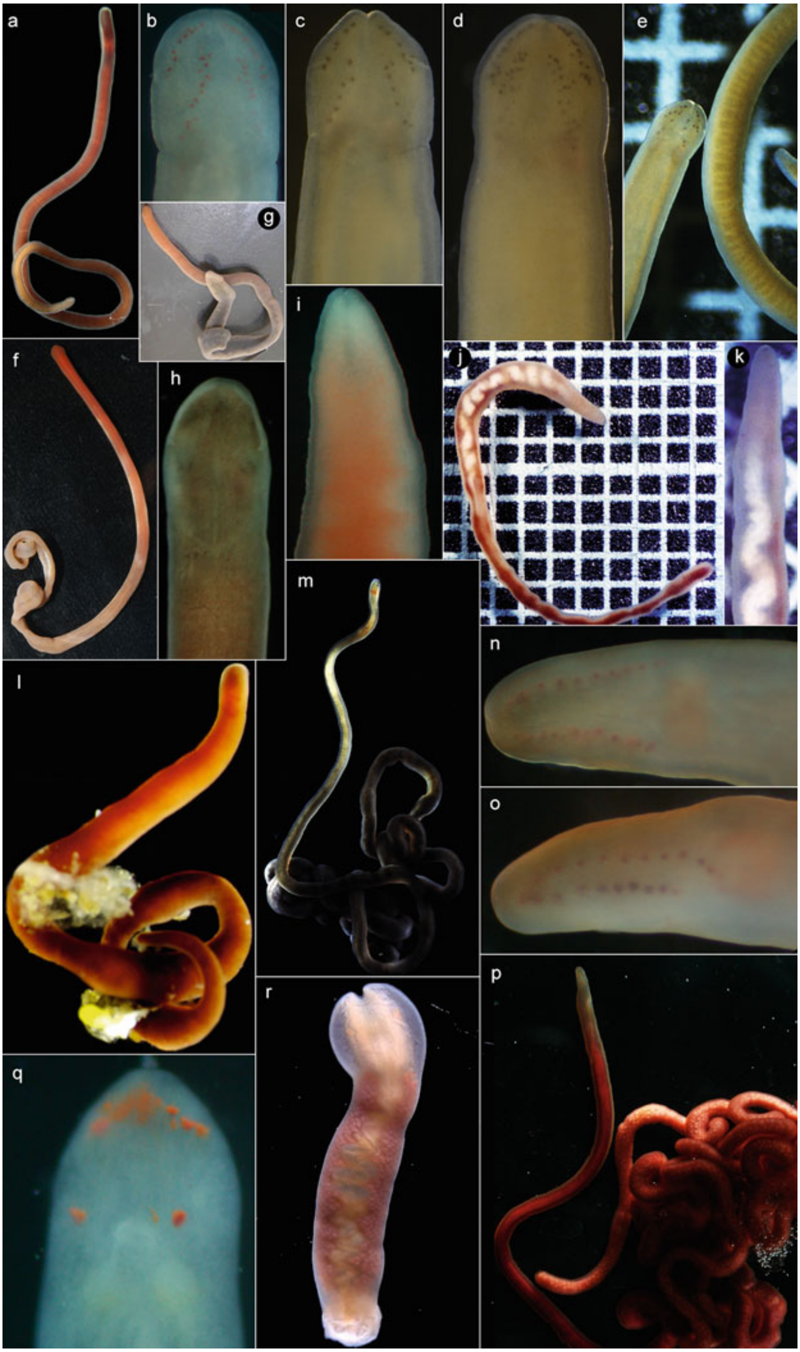

Fig. 16.4 **a** *Ramphogordius sanguineus*, Saijo. **b–g** *Amphiporus* spp.; **b** Shimoda. **c**, **d** Oshoro. **e** Otsuchi. **f** Misaki. (Photograph by H. Kohtsuka). **g** Amakusa. (Photograph by J. Inoue.) **h** *Amphiporus antifuscus*, Akkeshi. **i** *Ovicides paralithodis*, subtidal (215 m depth), from egg mass of *Paralithodes camtschaticus*, Abashiri. **j**, **k** *Diopsonemertes acanthocephala* (**j**, entire

16.4 Hoplonemertea

16.4.1 Monostilifera

A total of 44 species of monostiliferans are here considered as valid taxa; the actual diversity is expected to be nearly double the number, with at least 40 potentially undescribed species so far found in Japanese waters (Kajihara, unpublished data).

The '*Amphiporus cervicalis*' species complex contains at least two forms; they are common and abundant in the intertidal zones from Hokkaido to Kyushu. One morphotype is whitish, often tinged with a beige colour; the ocelli are either black or dark red (Fig. 16.4b–e). The other is anteriorly orange to red, sometimes posteriorly grayish (Fig. 16.4f, g). Potential nominal species to refer to those forms include *Polia cervicalis* Stimson, 1857; *Tatsnoskia depressa* Stimpson, 1857; *Amphiporus parvus* Yamaoka, 1940; *Amphiporus formidabilis* Griffin, 1898; *Amphiporus imparispinosus* Griffin, 1898; and *Amphiporus musculus* Iwata, 1954.

Amphiporus antifuscus Iwata, 1954 (Fig. 16.4h) is rarely found in Akkeshi. This species might be closely related to *Tortus tokmakovae* Chernyshev, 1991 (Kajihara, personal observation).

Amphiporus gelatinosus Coe, 1905 has been reported from Japan, but this record cannot be substantiated (Kajihara 2007).

Amphiporus insolitus Iwata, 1954 has a uniformly brown-coloured body, described from Kushimoto. It is herein regarded as a junior synonym of *Diplomma serpentina* (Stimpson, 1855).

Amphiporus reduncus Iwata, 1957 and *Amphiporus retrotumidus* Iwata, 1957, both described from Sagami Bay, are bulky species (10 cm in length, 7 mm in width), having an orange- or vermillion-coloured body (pale brownish yellow in preserved state) and 16 and 15 proboscis nerves, respectively. These characteristics are also found in *Nipponnemertes ogumai* (Yamaoka, 1947); the former two are herein synonymized with the latter.

Amphiporus regius Iwata, 1954 is only known by the original description from Muroran. It has four eyes, an orange-coloured body, and a black, Ш-shaped cephalic patch; it is apparently a variety of the '*Tetrastemma coronatum* complex.'

From decapod egg masses, two named, and one unnamed, species of monositliferans occur in Japanese waters: *Caricinonemertes mitsukurii* Takakura, 1910 from the Japanese mitten crab *Eriocheir japonica* (De Haan, 1835); *Ovicides*

Fig. 16.4 (continued) animal; **k**, head, lateral view), subtidal (59 m depth), Otsuchi Bay. **l** *Diplomma serpentina*, intertidal, Misaki. (Photograph by H. Kohtsuka.) **m** *Emplectonema gracile*, intertidal, Oshoro. **n**–**p** *Emplectonema kandai* (**n**, head, dorsal view; **o**, head, lateral view; **p**, entire animal), Misaki. **q** *Emplectonema mitsuii*, intertidal, Shimoda. **r** *Malacobdella japonica*, intertidal, within the mantle cavity of *Mactra sachalinensis*, Akkeshi. (After Alfaya et al. 2015.) (**a** Reproduced from Kajihara and Fujita 2008. **r** Reproduced from Alfaya et al. 2015) *paralithodis* Kajihara and Kuris, 2012 (Fig. 16.4i) from the red king crab *Paralithodes camtshaticus* (Tilesius, 1815); an undescribed form of non-carcinonemertid has been found from the callianassid *Glypturus armatus* (A. Milne-Edwards, 1870) (R. Yoshida, personal communication).

Diopsonemertes acanthocephala Kajihara et al., 2001 (Fig. 16.4j, k) is only known by the holotype collected among shell gravel at a depth of 59 m in Otsuchi Bay.

Diplomma serpentina (Stimpson, 1855) (Fig. 16.4l) is a common species widely distributed in Indonesia, Vietnam, the Philippines, and Japan (Chernyshev 2011; Kajihara et al. 2011a); the northernmost distribution range in Japanese waters is Misaki.

Emplectonema gracile (Johnston, 1837) (Fig. 16.4m) is widely distributed in the temperate intertidal zones on the Northern Hemisphere (Turbeville 2011), and is common in eastern Japan (Misaki, Nakaminato, Usujiri, Muroran, Oshoro, Akkeshi) (Kajihara, personal observation).

Emplectonema kandai Kato, 1939, so far only known by the original description from Asamushi, may be also distributed southward to Misaki (Fig. 16.4n–p).

Emplectonema mitsuii Yamaoka, 1947 (Fig. 16.4q) has been found in Shimoda, Misaki, Sado, and Oshoro (Kajihara, personal observation).

Coe's (1944) record of *Emplectonema buergeri* Coe, 1901 (type locality: Sitka, Alaska) based on fixed material from a depth of 250 m off Izu-Ôshima cannot be substantiated.

Malacobdella japonica Takakura, 1897 (Fig. 16.4r) is an entocommensal symbiont with the bivalve *Pseudocardium sachalinense* (Sehrenck, 1862), so far reported from the Pacific Coast of middle to eastern Japan, as well as Sakhalin (summarized in Kajihara 2007).

The terrestrial species *Geonemertes pelaensis* Semper, 1863 has previously been reported from the Ogasawara Islands. The species is also distributed in Ishigakijima Island, where it was observed to prey on the terrestrial isopod *Cubaris murina* Brandt, 1833 (T. Shimada, personal communication) (Fig. 16.5a).

Three nominal species of *Nipponnemertes* have been reported from Japanese waters: *N. bimaculata* (Coe, 1901), *N. ogumai* (Yamaoka, 1947) (Fig. 16.5b), and *N. punctatula* (Coe, 1905) (Fig. 16.5c). Undetermined, uniformly coloured forms, varying from red, pink, orange, pale yellow, and white, are found in Okinawa (among coral rubble at SCUBA-approachable depths), Shirahama (subtidal), and Sagami Bay (subtidal, down to 300 m). Cf. '*Cosmocephala*' *japonica* Stimpson, 1857 (Fig. 16.5d–h), possibly forming a cryptic species complex, is similar to *N. bimaculata*, but the dorsal surface is the same colour as the cephalic patch, unlike the reddish or orange colour in *N. bimaculata*. Kajihara et al.'s (2015) molecular phylogeny suggests that species in *Nipponnemertes* with and without a cephalic patch, respectively, form reciprocally monophyletic groups. Given that *N. drepanophoroides* Griffin, 1898 (lacking a cephalic patch) represents the type species for *Nipponnemertes* (see Kajihara 2007 for nomenclatural discussion), the forms with a cephalic patch (such as *N. bimaculata* and *N. punctatula*) may be classified in *Cosmocephala*, which should be investigated in future studies.

Fig. 16.5 **a** *Geonemertes pelaensis*, Ishigakijima. (Photograph by T. Shimada.) **b** *Nipponnemertes ogumai*, Izu. **c** *Nipponnemertes punctatula*, intertidal, Oshoro. **d–h** cf. '*Cosmocephala*' *japonica* (**d**, **e** subtidal, among cultured oysters, Hiroshima Bay; **f**, **g** subtidal, 90 m depth, Sagami Bay; **h** intertidal, Oshoro). **i** *Nemertellina yamaokai*, subtidal (6 m depth), Akkeshi. **j** *Nemertopsis*

Nemertellina yamaokai Kajihara et al., 2000 (Fig. 16.5i) is known from Akkeshi, as well as Peter the Great Bay (Chernyshev 2014), but a similar form with a much thinner body is distributed along the Pacific Coast of middle to eastern Japan (Kajihara, personal observation). The species is closely related to *Tetraneuronemertes lovgreni* Sundberg et al., 2007. The morphology of the latter indicates that the genus *Tetraneuronemertes* might be a junior synonym of *Nemertellina*.

Nemertopsis mitellicola Kajihara, 2007 (Fig. 16.5j) can be differentiated from *Nemertopsis quadripunctata* (Quoy and Gaimard, 1833) (Fig. 16.5k–m) by having a cephalic patch and fluted stylet; the latter species lacks the cephalic patch and has a smooth stylet. These are the two species of barnacle-associated monostiliferans distributed along the Pacific coasts of Japan. Undocumented, high diversity of *Nemertopsis* exists in Southeast Asia (S. Sun, personal communication).

Akhmatova et al. (2012) examined the species composition of *Oerstedia* in the Far Eastern Seas of Russia based on 28S rRNA sequences and allozyme (11 loci) analysis, indicating that *Oerstedia dorsalis* sensu Iwata (1954a) is a different taxon from *O. dorsalis* s. str. In addition to the two named species, *O. polyorbis* Iwata, 1954 (Fig. 16.5n) and *O. venusta* Iwata, 1954 (Fig. 16.5o), there are some other forms previously not reported from Japanese waters (Fig. 16.5p–r) (Kajihara, personal observation).

The genus *Ototyphlonemertes* contains about 23 named species of interstitial forms. From Japanese waters, the following 3 species have been reported: *O. martynovi* Chernyshev, 1993 (or '*duplex*'-morph) is widely distributed in Japanese waters; *O. dolichobasis* Kajihara, 2007 and *O. nikolaii* Chernyshev, 1998 (Fig. 16.6a) are only known from Otshuchi Bay, but the locality may have been destroyed by the 2011 tsunami.

Paranemertes incola Iwata, 1952 is only known by the holotype found under stones in Tomioka; the body is anteriorly chestnut brown, laterally and ventrally yellow, with numerous rings consisting of minute dark brown dots. *Paranemertes katoi* Yamaoka, 1947 is morphologically almost the same as *P. peregrina* Coe, 1901 (Fig. 16.6b–d). The latter is distributed on the northern Pacific Rim but may contain several cryptic species (Hao et al. 2015).

Three brackish-water species are known from eastern Japan: *Potamostoma shizunaiense* Kajihara et al., 2003 (Fig. 16.6e) (mouth of the Shizunai River, Hokkaido), *Sacconemertella lutulenta* Iwata, 1970 (Lake Hinuma, Ibaraki), and *Sacconemertopsis olivifera* Iwata, 1970 (Lake Hinuma, Ibaraki). Their phylogeny, in combination with *Sacconemertopsis belogurovi* Chernyshev, 1991 (Southern

Fig. 16.5 (continued) mitellicola, intertidal, among *Capitulum mitella*, Shirahama. **k**–**m** cf. *Nemertopsis quadripunctata* (**k** entire animal; **l** head, dorsal view; **m** central stylet and basis), intertidal, among holdfast of *Eisenia bicyclis*, Shimoda. **n** *Oerstedia polyorbis*, intertidal, Akkeshi. **o** *Oerstedia venusta* sensu Thollesson and Norenburg (2003), intertidal, Akkeshi. **p** *Oerstedia* sp., intertidal, Oshoro. **q** *Oerstedia* sp. subtidal, Akkeshi. **r** *Oerstedia* sp. subtidal (60 m depth), off Nagan'nu Island

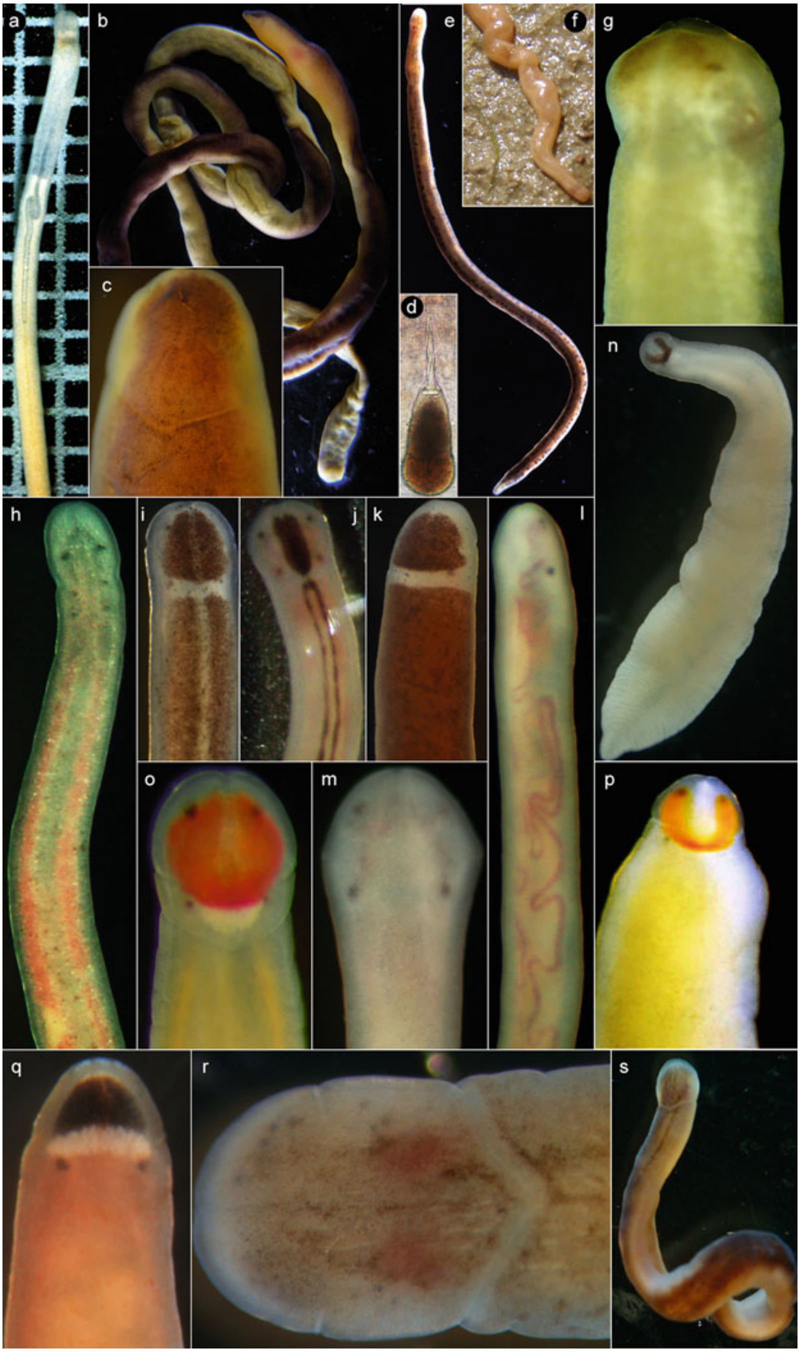

Fig. 16.6 **a** *Ototyphlonemertes nikolaii*, intertidal, Otsuchi Bay. **b**–**d** *Paranemertes peregrina* (**b** entire animal; **c** head, dorsal view; **d** central stylet and basis), intertidal, Oshoro. **e** *Potamostoma shizunaiense*, intertidal, Shizunai. (©Zoological Society of Japan.) **f**, **g** *Prosadenoporus spectaculus* (**f** entire animal in situ; **g** head, dorsal view), intertidal, Hanejinaikai (Okinawa).

Primorye, Russia), may provide insight into the biogeography of brackish-water organisms in this area and their marine–freshwater evolutionary dynamism in the Quaternary period.

Prosadenoporus spectaculus (Yamaoka, 1940) (listed as *Pantinonemrtes spectacula* in Kajihara 2007) was recently rediscovered at an intertidal mudflat in Hanejinaikai, Okinawa (Fig. 16.6f, g; R. Yoshida, personal communication.), but the precise habitat was not recorded in the original description.

The freshwater species *Prostoma ohmiense* Chernyshev et al., 1998 is supposedly endemic to Lake Biwa. It was described on the basis of a subtle morphological difference (ciliation in the oesophagus) from other species; its species status should be tested using DNA sequence data. The same is true for other forms reported from various localities in Japan under the names such as *Prostoma graecense* or *P. lac*[*u*] *stre* to determine their species identity (Fig. 16.6h).

Zaslavskaya et al. (2010) examined the taxonomic status of the five colour varieties of *Quasitetrastemma nigrifrons* (Coe, 1904) (Fig. 16.6i–k) and its closely related form *Quasitetrastemma stimpsoni* (Chernyshev, 1992) (Fig. 16.6l, m) based on 24 allozyme loci. Their results suggest that both are 'good species,' whereas one colour morph, *Q. nigrifrons* var. *pallidum*, contains a cryptic species.

Tetrastemma pimaculatum Chernyshev, 1998 (Fig. 16.6n) and *Tetrastemma roseocephalum* (Yamaoka, 1947) (Fig. 16.6o, p) are closely related to each other. *Tetrastemma pinnatum* Iwata, 1954 has characteristic 'swelling' of the epidermis on the lateral edges of the body; the species has never been discovered again even in the type locality, Oshoro (Kajihara, personal observation). Tetrastemmatids with a dark-coloured cephalic patch (e.g., Fig. 16.6q) so far reported from Japan include *T. insolens* Iwata, 1952, *T. melanocephalum* sensu Yamaoka (2005), *Prostoma coronatum* sensu Yamaoka (1940), *Tetrastemma coronatum* sensu Iwata (1954a), and *Tetrastemma verinigrum* Iwata, 1954. These forms, together with *T. candidum* sensu Iwata (1954a) (no cephalic patch), require DNA taxonomy to scrutinize their taxonomic identity. Eight species of potentially undescribed tetrastemmatids have been confirmed in Japanese waters, mostly in the Nansei Islands (Kajihara, personal observation).

Tortus tokmakovae Chernyshev, 1991 (Fig. 16.6r, s) is herein added as a new member of the Japanese ribbon worms. The species is rarely found in Akkeshi.

There are three named species in *Zygonemertes* from Japanese waters, all are from Hokkaido: *Z. glandulosa* Yamaoka, 1940, *Z. jamsteci* Kajihara, 2002 (Fig. 16.7a, b), and *Z. shintai* Kajihara, 2002 (Fig. 16.7c). Clarifying species

Fig. 16.6 (continued) (Photograph by R. Yoshida.) **h** *Prostoma* sp. Hokkaido University Botanical Garden, Sapporo. **i–k** *Quasitetrastemma nigrifrons*, intertidal (**i** var. *bimaculatum*, Oshoro; **j** var. *pallidum*, Akkeshi; **k** var. *spadix*, Shimoda). **l**, **m** *Quasitetrastemma stimpsoni* (**l** anterior body, lateral view; **m** head, dorsal view), intertidal, Akkeshi. **n** *Tetrastemma pimaculatum*, intertidal, Oshoro. **o**, **p** *Tetrastemma roseocephalum* (**o** Oshoro; **p** Misaki). (Photograph by H. Kohtsuka.) **q** *Tetrastemma* sp. intertidal, Esashi. **r**, **s** *Tortus tokmakovae* (**r** head, dorsal view; **s** entire animal), Akkeshi. (**e** Reproduced from Kajihara et al. 2003)

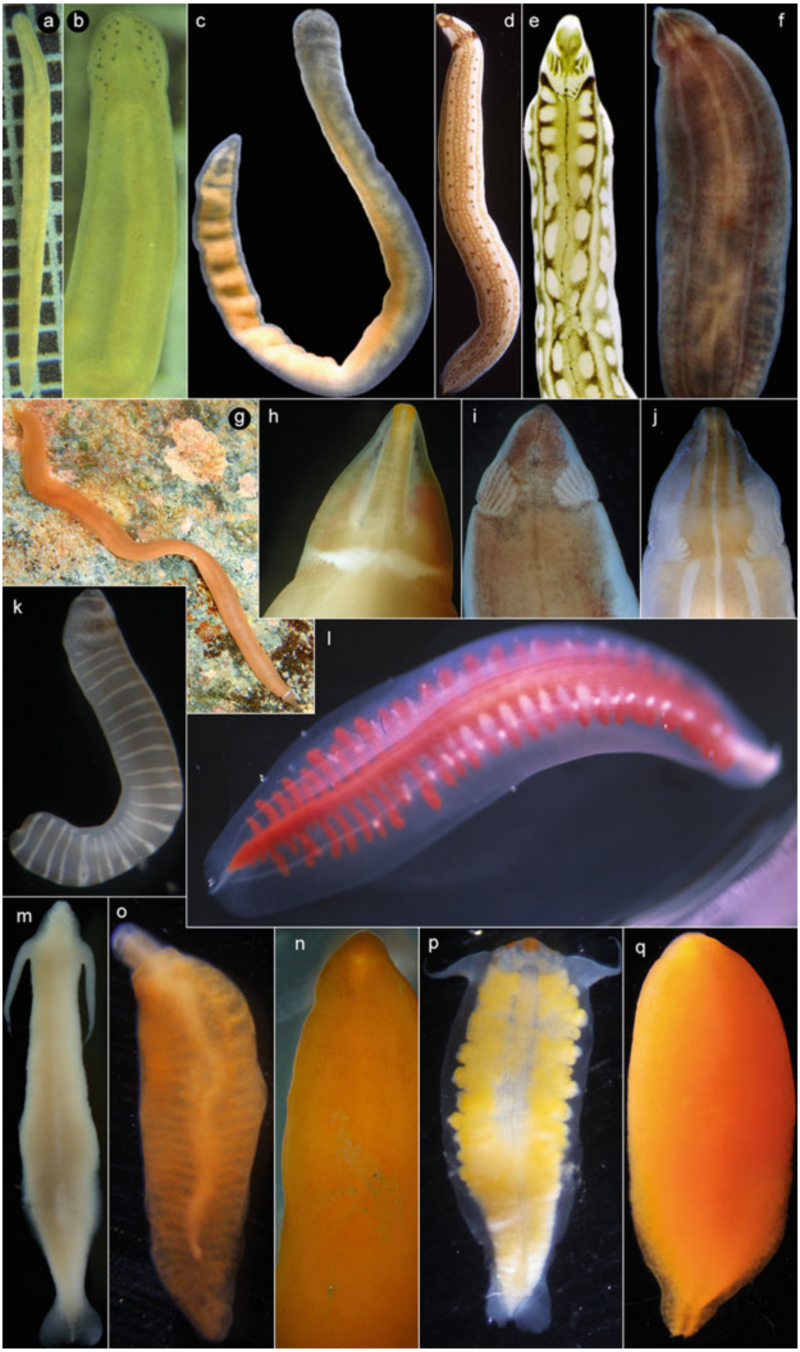

Fig. 16.7 **a**, **b** *Zygonemertes jamsteci*, intertidal, Akkeshi. **c** *Zygonemertes shintai*. (©Japanese Society of Systematic Zoology.) **d**–**k** Unidentified reptantians: **d** subtidal (50 m), Nansei Islands; **e** subtidal (80 m), off Jôgashima. (Photograph by H. Kohtsuka.) **f** subtidal, Nansei Islands.

diversity of congeners in Honshu and southern areas requires DNA taxonomy, because they are externally quite similar to each other, mostly having a pale yellow to green body colour.

16.4.2 Polystilifera

16.4.2.1 Reptantia

Only three species of reptantians have been reported from Japanese waters; all are only known by the holotype dredged from 50 to 130 m depth in Sagami Bay. *Drepanophorus longiceps* Iwata, 1957 is 1.5 cm long and 2 mm wide; the intestine is orange in life. *Kameginemertes parmiornata* (Iwata, 1957) is only known from the preserved state; the body is 2.5 cm long and 2 mm wide, pale orange dorsally, yellowish white ventrally; with a shield-shaped brown cephalic patch. *Sagaminemertes nagaiensis* (Iwata, 1957) is also known by a preserved specimen, which was 7 cm long and 5 mm wide; a round, dark brown cephalic patch is present; the cephalic furrow is also dark brown; the body is dorsally pale brown, ventrally pale yellow. At least ten species of undetermined reptantians, mostly in the Nansei Islands, are awaiting formal description (Fig. 16.7d–k) (Kajihara, unpublished data).

16.4.2.2 Pelagica

Four species of pelagic polystiliferans have been reported from Japanese waters: *Dinonemertes shinkaii* Kajihara and Lindsay, 2010 (Fig. 16.7l); *Nectonemertes mirabilis* Verrill, 1892 (Fig. 16.7m) (*N. japonica* Foshay, 1912 is tentatively synonymized); *Pelagonemertes moseleyi* Bürger, 1895; and *Protopelagonemertes beebei* Coe, 1936 (Fig. 16.7n). No fewer than four species of undetermined pelagic polystiliferans have been found in Japanese waters (Fig. 16.7o–q; K. Kakui, personal communication).

Fig. 16.7 (continued) (Photograph by K. Kakui.) **g**, **h** Intertidal, Kunigami-son. (Photograph by R. Yoshida.) **i** Subtidal, off Iwate. (Photograph by K. Kakui.) **j** Intertidal, Awasehigata, Okinawa. (Photograph by R. Yoshida.) **k** Subtidal, Nansei Islands. (Photograph by K. Kakui.) **l** *Dinonemertes shinkaii*, 2343 m, off Iwate Prefecture. (© Magnolia Press.) (Photograph by D. J. Lindsay.) **m** *Pelagonemertes moselyi*, Nansei Islands. **n** *Protopelagonemertes beebei*, about 1100 m, Sagami Bay. (Photograph by D.J. Lindsay.) **o–q** Pelagica spp. (Photograph by K. Kakui.) (**c** Reproduced from Kajihara 2002; **i** reproduced from Kajihara and Lindsay 2010)

16.5 Summary

A total of 126 species of nemerteans have been reported from Japanese waters, which still harbour at least 77 forms of unreported (potentially undescribed) taxa (Kajihara, unpublished data). The number of known/unknown species in each taxon, and the faunal 'clarification rate,' are Palaeonemertea (12/5, 71 %), Pilidiophora (63/18, 78 %), Monostilifera (44/40, 52 %), Reptantia (3/10, 23 %), and Pelagica (4/4, 50 %).

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References

Akhmatova AF, Chernyshev AV, Zaslavskaya NI (2012) The species composition of the nemertean genus *Oerstedia* (Nemertea: Hoplonemertea) in the Far Eastern seas of Russia. Russ J Mar Biol 38:423–430

Alfaya JEF, Bigatti G, Kajihara H, Strand M, Sundberg P, Machordom A (2015) DNA barcoding supports identification of *Malacobdella* species (Nemertea: Hoplonemertea). Zool Stud 54:10

Andrade SCS, Strand M, Schwartz M, Chen H-X, Kajihara H, von Döhren J, Sun S-C, Junoy J, Thiel M, Norenburg JL, Turbeville JM, Giribet G, Sundberg P (2012) Disentangling ribbon worm relationships: multi-locus analysis supports traditional classification of the phylum Nemertea. Cladistics 28:141–159

Andrade SCS, Montenegro H, Strand M, Schwartz ML, Kajihara H, Norenburg JL, Turbeville JM, Sundberg P, Giribet G (2014) A transcriptomic approach to ribbon worm systematics (Nemertea): resolving the Pilidiophora problem. Mol Biol Evol 31:3206–3215

Asakawa M, Ito K, Kajihara H (2013) Highly toxic ribbon worm *Cephalothrix simula* containing tetrodotoxin in Hiroshima Bay, Hiroshima Prefecture, Japan. Toxins 5:376–395

Chen H-X, Strand M, Norenburg JL, Sun S-C, Kajihara H, Chernyshev AV, Maslakova SA, Sundberg P (2010) Statistical parsimony networks and species assemblages in cephalotrichid nemerteans (Nemertea). PLoS One 5:e12885

Chernyshev AV (2008) Fauna of nemerteans of Amursky Bay and the adjacent areas. In: Lutaenko KA, Vaschenko MA (eds) Ecological studies and the state of the ecosystem of Amursky Bay and the estuarine zone of the Razdolnaya River (Sea of Japan). Dalnauka, Vladivostok, pp 267–278

Chernyshev AV (2011) Nemertean worms (Nemertea) on the Vietnamese coastal waters. In: Anonymous (ed) Coastal marine biodiversity and bioresources of Vietnam and adjacent areas to the South China Sea. Vladivostok and Nha Trang, Dalnauka, pp 21–25

Chernyshev AV (2014) Nemertean biodiversity in the Sea of Japan and adjacent areas. In: Sun S, Adrianov AV, Lutaenko KA, Sun X-X (eds) Marine biodiversity and ecosystem dynamics of the Northwest Pacific Ocean. Science Press, Beijing, pp 119–135

Chernyshev AV (2015) CLSM analysis of the phalloidin-stained muscle system of the nemertean proboscis and rhynchocoel. Zool Sci 32:547–560

Chernyshev AV (2016) Nemerteans of the coastal waters of Vietnam. In: Adrianov AV, Lutaenko KA (eds) Biodiversity of the western part of the South China Sea. Dalnauka, Vladivostok, pp 279–314

Coe WR (1901) Papers from the Harriman Alaska Expedition. XX. The nemerteans. Proc Wash Acad Sci 3:1–84

Coe WR (1940) Revision of the nemertean fauna of the Pacific coasts of North, Central, and northern South America. Allan Hancock Pac Exped 2:247–322

Coe WR (1944) Geographical distribution of the nemerteans of the Pacific coast of North America, with descriptions of two new species. J Wash Acad Sci 34:27–32

Fernández-Álvarez FÁ, Machordom A (2013) DNA barcoding reveals a cryptic nemertean invasion in Atlantic and Mediterranean waters. Helgol Mar Res 67:599–605. doi:10.1007/s10152-013-0346-3

Hao Y, Okazaki RK, Kajihara H, Chernyshev AV, Sun S-C (2015) DNA taxonomy of *Paranemertes* (Nemertea: Hoplonemertea) with spirally fluted stylets. Zool Sci 32:571–578

Hiebert TC, Maslakova SA (2015) Integrative taxonomy of the *Micrura alaskensis* Coe, 1901 species complex (Nemertea: Heteronemertea), with descriptions of a new genus *Maculaura* gen. nov. and four new species from the NE Pacific. Zool Sci 32:615–637

Iwata F (1954a) The fauna of Akkeshi Bay. XX. Nemertini in Hokkaido (revised report). J Fac Sci Hokkaido Univ Ser 6 Zool 12:1–39

Iwata F (1954b) Invertebrate fauna of the intertidal zone of the Tokara Islands. X. Nemertini. Publ Seto Mar Biol Lab 4:27–31

Iwata F (1957) Nemerteans from Sagami Bay. Publ Akkeshi Mar Biol Stat 7:1–31

Kajihara H (2002) Two new species of Zygonemertes (Nemertea: Enopla: Monostilifera) from Hokkaido, Japan. Species Divers 7:121–143

Kajihara H (2006) Four palaeonemerteans (Nemertea: Anopla) from a tidal flat in middle Honshu, Japan. Zootaxa 1163:1–47

Kajihara H (2007) A taxonomic catalogue of Japanese nemerteans (phylum Nemertea). Zool Sci 24:287–326

Kajihara H (2015) A histology-free description of the branched-proboscis ribbonworm *Gorgonorhynchus albocinctus* sp. nov. (Nemertea: Heteronemertea). Publ Seto Mar Biol Lab 43:92–102

Kajihara H, Fujita Y (2008) Kabutogani shiiku suisou chuu ni tairyou hassei shita moede himomushi (shinshou). Umiushi Tsushin 58:10–11 [in Japanese]

Kajihara H, Ise Y (2008) Morphology of Lineopselloides albilineus (Nemertea: Heteronemertea: Lineidae) from Japanese waters, with complementary redescription of the holotype. Bull Kitakyushu Mus Nat Hist Hum Hist Ser A 6:1–12

Kajihara H, Lindsay DJ (2010) Dinonemertes shinkaii sp. nov., (Nemertea: Hoplonemertea: Polystilifera) a new species of bathypelagic nemertean. Zootaxa 2429:43–51

Kajihara H, Kuris AM (2013) *Ovicides paralithodis* (Nemertea, Carcinonemertidae), a new species of symbiotic egg predator of the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Decapoda, Anomura). ZooKeys 258:1–15

Kajihara H, Nishi E (2013) First record of *Euborlasia nigrocincta* Coe, 1940 (Nemertea: Heteronemertea) from the western Pacific. Check List 9:826–828

Kajihara H, Gibson R, Mawatari SF (2003) *Potamostoma shizunaiense* gen. et sp. nov. (Nemertea: Hoplonemertea: Monostilifera): a new brackish-water nemertean from Japan. Zool Sci 20: 491–500

Kajihara H, Chernyshev AV, Sun S-C, Sundberg P, Crandall FB (2008) Checklist of nemertean genera and species published between 1995 and 2007. Species Divers 13:245–274

Kajihara H, Olympia M, Kobayashi N, Katoh T, Chen H-X, Strand M, Sundberg P (2011a) Systematics and phylogeny of the hoplonemertean genus *Diplomma* (Nemertea) based on molecular and morphological evidence. Zool J Linn Soc 161:695–722

Kajihara H, Yamasaki H, Andrade SCS (2011b) *Carinoma hamanako* sp. nov. (Nemertea: Palaeonemertea), the first representative of the genus from the Northwest Pacific. Species Divers 16:149–165

Kajihara H, Yoshida R, Uyeno D (2012) First record of *Baseodiscus mexicanus* (Bürger, 1893) (Nemertea: Heteronemertea) from Japanese waters. Check List 8:754–755

Kajihara H, Sun S-C, Chernyshev AV, Chen H-X, Ito K, Asakawa M, Maslakova SA, Norenburg JL, Strand M, Sundberg P, Iwata F (2013) Taxonomic identity of a tetrodotoxin-accumulating ribbon-worm *Cephalothrix simula* (Nemertea: Palaeonemertea): a species artificially introduced from the Pacific to Europe. Zool Sci 30:985–997

Kajihara H, Kakui K, Yamasaki H, Hiruta SF (2015) *Tubulanus tamias* sp. nov. (Nemertea: Palaeonemertea) with two different types of epidermal eyes. Zool Sci 32:596–604

Kajihara H, Hosokawa I, Hosokawa K, Yoshida R (2016) Records of *Notospermus tricuspidatus* (Quoy & Gaimard, 1833) (Nemertea: Pilidiophora) in Japanese waters, with a review of warm-water green-bodied heteronemerteans from the Indo-West-Pacific. Fauna Ryukyuana 28:59–65

Kang X-X, Fernández-Álvarez FÁ, Alfaya JEF, Machordom A, Strand M, Sundberg P, Sun S-C (2015) Species diversity of *Ramphogordius sanguineus*/*Lineus ruber*-like nemerteans (Nemertea: Heteronemertea) and geographic distribution of *R. sanguineus*. Zool Sci 32: 579–589

Kvist S, Laumer CE, Junoy J, Giribet G (2014) New insights into the phylogeny, systematics and DNA barcoding of Nemertea. Invertebr Syst 28:287–308

Langerhans P (1880) Die Wurmfauna von Madeira III. Z Wiss Zool 34:87–143

Manchenko GP, Kulikova VI (1996) Allozyme and colour differences between two sibling species of the heteronemertean *Lineus torquatus* from the Sea of Japan. Mar Biol 125:687–691

McDermott JJ, Roe P (1985) Food, feeding behavior and feeding ecology of nemerteans. Am Zool 25:113–125

Schwartz ML (2009) Untying a Gordian knot of worms: systematics and taxonomy of the Pilidiophora (phylum Nemertea) from multiple data sets. Columbian College of Arts and Sciences, The George Washington University, Washington, DC

Senz W (1997) Morphologie und klassifikatorische Position einiger anopler Nemertinen (Nemertini: Anopla). Ann Naturhist Mus Wien 99B:423–496

Shynu SP, Shibu S, Jayaprakas V (2015) First record of nemertean *Lineus mcintoshii* (Nemertea: Anopla: Heteronemertea) from the Indian coast. Mar Biodivers Rec 8:e25

Sundberg P, Gibson R (1995) The nemerteans (Nemertea) of Rottnest Island, western Australia. Zool Scr 24:101–141

Takakura U (1898) Misaki kinbousan himomushirui (Nemertine) no bunrui [A classification of the nemerteans in the vicinity of Misaki]. Zool Mag 10:38–44, 116–120, 184–187, 331–337, 424–429 [in Japanese]

Thollesson M, Norenburg JL (2003) Ribbon worm relationships: a phylogeny of the phylum Nemertea. Proc R Soc B Biol Sci 270:407–415

Turbeville JM (2011) The first record of *Emplectonema gracile* (Nemertea: Hoplonemertea) on the Atlantic coast of North America. Mar Biodivers Rec 4:e89

Yamaoka T (1940) The fauna of Akkeshi Bay. IX. Nemertini. J Fac Sci Hokkaido Imp Univ Ser 6 Zool 7:205–263

Yamaoka T (2005) On fourteen monostiliferous hoplonemerteans from the Izu Peninsula, Middle Japan. Publ Seto Mar Biol Lab 40:141–158

Zaslavskaya NI, Akhmatova AF, Chernyshev AV (2010) Allozyme comparison of the species and colour morphs of the nemertean genus *Quasitetrastemma* Chernyshev, 2004 (Hoplonemertea: Tetrastemmatidae) from the Sea of Japan. J Nat Hist 44:2303–2320

Chapter 17
Review of the Studies of Japanese Entoprocts (Entoprocta)

Tohru Iseto

Abstract The study of entoprocts in Japanese waters was begun in 1890 by Asajiro Oka, who described 1 colonial species from central Japan. To date, 30 solitary and 11 colonial species have been reported from the northern subarctic (Hokkaido) to the southern subtropics (Okinawa) of Japan. This chapter provides a review of the diversity of entoprocts in Japan and summarizes interesting aspects of this animal group as revealed by the studies of Japanese entoprocts, such as reproductive strategies, variations and benefits of commensalism, and phylogeny. Current problems of their taxonomy are also discussed.

Keywords Marine invertebrates • North Pacific • Symbiosis • Systematics • Sessile organism • Anthropogenic disturbance

17.1 Introduction to the Phylum Entoprocta

Entoprocts (=kamptozoans) are small benthos living in oceans worldwide (Wasson 2002). A few species live in brackish waters, and only two have been reported from freshwater. Entoprocts are colonial or solitary, with either form having the same basic body plan composed of calyx, stalk, and basal attaching apparatus (Fig. 17.1). The calyx is the main body of the animal, containing digestive organs, brain, gonads, a pair of protonephridia, and a tentacle crown on the top. The stalk is often flexible, allowing the animal to actively bend or twist its body. At the base of the stalk, solitary species have a foot, which is an attaching apparatus with gland cells, whereas colonial species usually have a stolon that connects the clonal individuals. Most colonial species have a circulatory organ called the star-cell complex at the interface of the calyx and the stalk (Emschermann 1969). Solitary species are often commensal on a variety of hosts such as polychaetes, sponges, and

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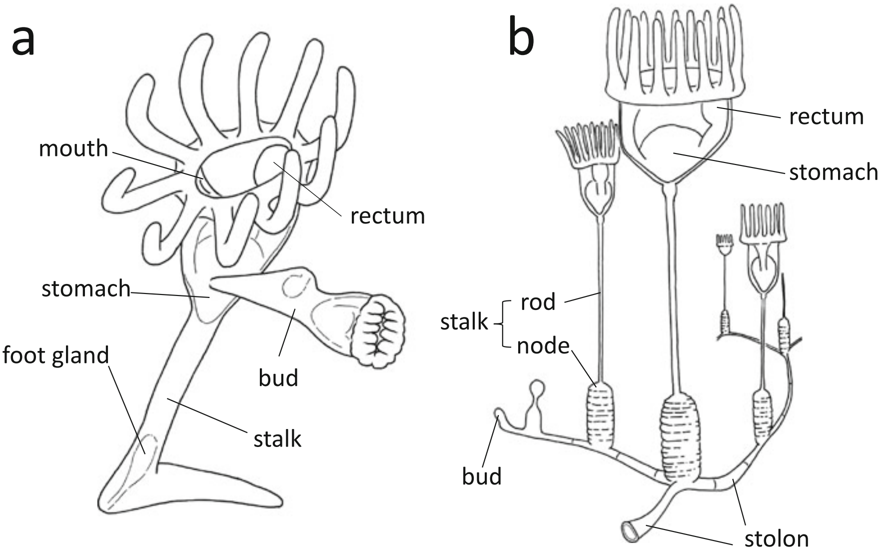

Fig. 17.1 Schematic drawings of entoprocts: (**a**) solitary form; (**b**) colonial form. (Reproduced from Iseto 2005a)

bryozoans, whereas colonial species are usually not commensal and live nonspecifically on hard substrata such as shells, rocks, and algae.

Emschermann (1972) proposed a division of Entoprocta into two orders, Solitaria and Coloniales, comprising all solitary and colonial species, respectively. This dichotomy is practical and has been used in various publications. However, one of the colonial families, Loxokalypodidae, does not share some characteristics (e.g., star-cell complex) with the other two colonial families but is similar to solitary groups in its larval morphology instead (Nielsen 1989). The position of the family Loxokalypodidae therefore needs to be extensively analyzed to judge the validity of dichotomy of Solitaria and Coloniales. In the present article, I adopt the following scheme, with only four families under the phylum Entoprocta.

Entoprocta Nitsche, 1870 (Kamptozoa Cori, 1929)

Loxosomatidae Hincks, 1880

Loxosoma Keferstein, 1862
Loxosomella Mortensen, 1911
Loxomitra Nielsen, 1964

Loxokalypodidae Emschermann, 1972

Loxokalypus Emschermann, 1972

Barentsiidae Emschermann, 1972

Barentsia Hincks, 1880

Coriella Kluge, 1946
Pedicellinopsis Hincks, 1884
Pseudopedicellina Toriumi, 1951
Urnatella Leidy, 1851

Pedicellinidae Johnston, 1847

Pedicellina Sars, 1835
Loxosomatoides Annandale, 1908
Myosoma Robertson, 1900
Sangavella du Bois-Reymond-Marcus, 1957

17.2 History of Entoproct Studies in Japan

The study of entoprocts in Japanese waters was started by Asajiro Oka (1890), who described a colonial species, *Ascopodaria misakiensis*, from Misaki, central Japan (Fig. 17.2). In 1895, he published a detailed description of the same species under

Fig. 17.2 Major study sites of entoprocts in Japan

the name of *Barentsia misakiensis*, which is now considered a junior synonym of *B. discreta* (Busk, 1886). After a long hiatus since Oka's study on entoprocts, Okada and Mawatari (1938) reported *B. discreta* from Shirahama in Wakayama Prefecture. Thereafter, Toriumi (1944, 1949, 1951) and Yamada (1956) reported several colonial and solitary entoproct species, respectively, from Tohoku and Hokkaido in northern Japan. Among these, *Loxosomella shizugawaensis* (Toriumi, 1949) was the first solitary entoproct reported from Japan. Mukai and Makioka (1978, 1980) reported regeneration and sex differentiation of *B. discreta* based on their experiments in Shimoda, middle of Japan.

Konno (1972) collected a curious loxosomatid species, *Loxosomella bifida* Konno, 1972, by plankton net that had a pair of 'legs' (Fig. 17.3a–c) and could 'walk' like humans. Discovery of this species led Konno to become further involved in the study of entoprocts (Konno, personal communication). He described 14 new solitary species associated with polychaetes from Fukaura, Japan (Konno 1972, 1973a, b, 1974, 1975, 1976, 1977a, b; Konno 1978). Konno (1978, 1985, 1990b) also surveyed entoprocts around Japan and also reported some of the species he had originally described from Fukaura from other regions.

I collected entoprocts using glass slides as settlement substrata from a shallow coral reef area in Okinawa and discovered 12 noncommensal loxosomatids (Iseto 2001, 2002, 2003, 2006). This method enabled me to carry out a quantitative survey of entoprocts. I, with my coworkers, reported the annual abundance and reproduction of the noncommensal species from Okinawa (Iseto et al. 2007). In addition, Iseto et al. (2008) described a commensal species from Okinawa, living on sponges on a reef slope. Sugiyama et al. (2010) reported the annual field monitoring of the same species using SCUBA and revealed the population dynamics and reproduction strategies of the colony on the sponges. Iseto and Hirose (2010) detailed the comparative morphology of the foot structure of four genera of solitary entoprocts, which provided insights into the generic-level classification (discussed next).

A high school student, Osamu Ikeda, first found a freshwater species, *Urnatella gracilis*, in Japan in Saitama Prefecture in September 1974 (Ikeda et al. 1977).

Yokobori et al. (2008) reported the first full mitochondrial genome of two solitary species from Okinawa. Fuchs et al. (2010) reported the first molecular analyses of the internal phylogeny of Entoprocta using several species including some from Japan, and revealed inconsistencies between current taxonomy and molecular phylogeny, particularly for the genus *Loxosomella*. Recently, Kajihara et al. (2015) added *Loxosoma axisadversum* Konno, 1972, to the molecular phylogeny and postulated a non-monophyly of the genus *Loxosoma*.

A total of 41 entoproct species have been reported from Japan, and these have contributed to various aspects of entoproct studies. However, there remain immeasurable opportunities for new discoveries in the entoprocts living in Japan. In this chapter, the present knowledge about Japanese entoprocts is summarized, highlighting the aspects that are still unknown.

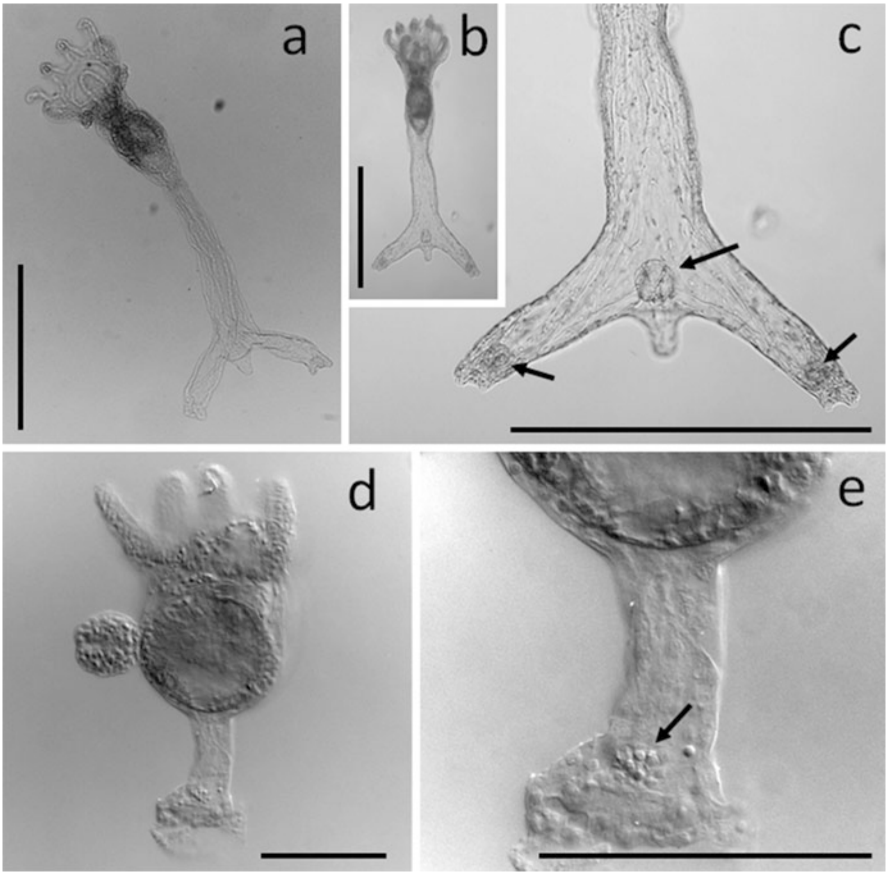

Fig. 17.3 Some type specimens of loxosomatids described by Konno. (**a**) Holotype of *Loxosomella bifida*. (**b**) A paratype specimen of *Loxosomella bifida*; *arrows* indicate foot glands. (**c**) High magnification of foot part of **b**. (**d**) Holotype of *Loxosomella poculi*. (**e**) High magnification of foot part of (**d**); foot gland cell mass indicated by *arrow*. *Scales* **a–c** 500 μm; **d**, **e** 100 μm

17.3 Systematic Accounts

17.3.1 Solitary Genera and Their Occurrence in Japan

All solitary species of entoprocts belong to the family Loxosomatidae. To date, more than 130 loxosomatids have been described from around the world, of which 30 species are reported from Japan (Table 17.1). The major study sites of solitary species are Akkeshi, Matsushima Bay, Fukaura, Misaki, Shimoda, Shirahama, and Okinawa (Fig. 17.2).

The genus *Loxosoma* is characterized by having a disc-shaped foot or sucking disc. Twenty-six species have been described from around the world (summarized

Table 17.1 List of solitary entoprocts found from Japan

Species	Locality	Host (P = polychaete, S = sponge)	Habitat	Depth (m)	Maximum total length (μm)	Type specimen	References
Loxomitra mizugamaensis Iseto, 2002	Okinawa	None	Nonliving substrata	1	1114	NSMT-Ka 34	Iseto (2002, 2007)
Loxomitra ryukyuensis Iseto, 2006	Okinawa	None	Nonliving substrata	4	2326	NSMT-Ka 74	Iseto (2006, 2007)
Loxomitra tetraorganon Iseto, 2002	Okinawa	none	Nonliving substrata	1–4	1200	NSMT-Ka 39	Iseto (2002, 2007)
Loxosoma axisadversum Konno, 1972	Fukaura	P (body)	Maldanidae > *Nicomache minor*, *N. personata*	0–1	230	NSMT-Ka 1	Konno (1972, 1978, 1985) and Kajihara et al. (2015)
Loxosoma cubitus Konno, 1974	Fukaura	P (body)	Terebellidae > *Thelepus* sp.	0–1	910	NSMT-Ka 6	Konno (1974, 1985)
Loxosoma monilis Konno, 1973	Fukaura	P (tube)	Maldanidae > Clymenella complanata	0–1	3426	NSMT-Ka 5	Konno (1973)
Loxosoma okudai Yamada, 1956	Akkeshi	P (body)	*Scalibregma inflatum*	–	560	Not located	Yamada (1956)
Loxosoma vatilli Konno, 1977	Fukaura, Noto	P (body/tube)	Capitellid polychaete, *Dasybranchus caducus*	0–1	1070	NSMT-Ka 8	Konno (1977a, 1978)
Loxosomella akkeshiensis (Yamada 1956)	Akkeshi, Shiriuchi, Fukaura	P (body)	Terebellidae > *Amphitrite cirrata*, *Lanice conchilega*	0–1	1840	Not located	Yamada (1956) and Konno (1973, 1985, 1990b)
Loxosomella allax (Iseto, 2002)	Okinawa	None	Nonliving substrata	1–4	1317	NSMT-Ka 44	Iseto (2002)

Loxosomella aloxiata Iseto, 2001	Okinawa	None	Nonliving substrata	1	1600	NSMT-Ka 29	Iseto (2001)
Loxosomella ampullae Konno, 1976	Fukaura	P (tube)	Terebellidae > *Thelepus setosus*	0–1	660	NSMT-Ka 9	Konno (1976, 1978)
Loxosomella bifida Konno, 1972	Fukaura	P (tube)	Terebellidae > *Neoleprea* cf. *amoyensis*	0–1	1420	NSMT-Ka 2	Konno (1972, 1978)
Loxosomella collumnodi Konno, 1976	Fukaura	P (tube)	Terebellidae > *Streblosoman japonica*	0–1	600	NSMT-Ka 11	Konno (1976)
Loxosomella dicotyledonis Iseto, 2003	Okinawa	None	Nonliving substrata	1	900	NSMT-Ka 71	Iseto (2003)
Loxosomella difigurata Konno, 1972	Fukaura	P (tube)	Terebellidae > *Neoleprea* cf. *amoyensis*	0–1	690	NSMT-Ka 3	Konno (1972, 1978)
Loxosomella intragemmata Iseto, 2003	Okinawa	None	Nonliving substrata	1	1260	NSMT-Ka 64	Iseto (2003)
Loxosomella lappa Iseto, 2001	Okinawa	None	Nonliving substrata	1	480	NSMT-Ka 25	Iseto (2001)
Loxosomella lecythifera Iseto, 2003	Okinawa	None	Nonliving substrata	1	1650	NSMT-Ka 55	Iseto (2003)
Loxosomella monocera Iseto, 2001	Okinawa	None	Nonliving substrata	1	420	NSMT-Ka 20	Iseto (2001)
Loxosomella parvipes Iseto, 2006	Okinawa	None	Nonliving substrata	1	1051	NSMT-Ka 83	Iseto (2006)

(continued)

Table 17.1 (continued)

Species	Locality	Host (P = polychaete, S = sponge)	Habitat	Depth (m)	Maximum total length (μm)	Type specimen	References
Loxosomella pistilli Konno, 1975	Fukaura	P (tube)	Eunicidae > *Palola siciliensis*	0–1	1085	NSMT-Ka 7	Konno (1975)
Loxosomella plakorticola Iseto & Sugiyama, 2008	Okinawa	S	*Plakortis*	11	1226	NSMT-Ka 87	Iseto et al. (2008)
Loxosomella poculi Konno, 1977	Fukaura	P (body)	Capitellidae > *Dasybranchus caducus*	0–1	280	NSMT-Ka 12	Konno (1977b, 1978)
Loxosomella pseudocompressa Konno, 1977	Fukaura	P (body)	Polynoidae > *Lepidasthenia interrupta*, *L. longissima*	0–1	555	NSMT (not confirmed)	Konno (1977b, 1985)
Loxosomella shizugawaensis (Toriumi, 1949)	Shizugawa Bay, Asamushi	None	Algae (Laminaria), sponges, mollusk shells, test of solitary ascidians	1	1500	Not located	Toriumi (1949, 1971, 1978, 1985)
Loxosomella spiropedis Konno, 1972	Fukaura, Shiriuchi	P (body)	Terebellidae > *Terebella* near *ehlenbergi*	0–1	370	NSMT-Ka 4	Konno (1972, 1978, 1985, 1990b)
Loxosomella stomatophora Iseto, 2003	Okinawa	None	Nonliving substrata	1	780	NSMT-Ka 52	Iseto (2003)
Loxosomella studiosorum (Toriumi, 1951)	Matsushima Bay	S	Monaxon sponge	–	660	Biological Institute, Tohoku University (Not confirmed)	Toriumi (1951)
Loxosomella umeri Konno, 1976	Fukaura	P (tube)	Terebellidae > *Thelepus setosus*	0–1 m	920	NSMT-Ka 10	Konno (1976, 1978, 1985)

NSMT National Science Museum, Tokyo (current name: National Museum of Nature and Science, Tokyo) in Nielsen 1996, 2010). This genus has a special affinity to polychaetes and is typically found attached to their body or inside their tube. Only one exceptional species, *L. isolata* Salvini-Plawen, 1968, was found interstitially (Salvini-Plawen, 1968); and the habitat of 1 species, *L. jaegersteni*, is unknown. Five species associated with polychaetes have been found in Japan (Table 17.1).

Loxosmella is the largest genus in Entoprocta, and more than 100 species have been described from around the world. This genus possesses a foot having a 'foot gland,' an organ composed of multiple gland cells. Most species, including the type species of this genus (*Loxosomella crassicauda* Salensky, 1877), have a foot groove under the foot that connects to the foot gland at the frontal end. However, the definition of this genus has been ambiguous, and the genus often includes some species having a different type of foot (discussed next). Twenty-two species of *Loxosomella* have been described from Japan. Among these, 10 species were found with polychaetes and 2 were found on sponges. The other 10 species are noncommensal.

The genus *Loxomitra* has a foot with only a pair of tiny expansions called terminal wings on the lateral side of the foot tip (Iseto 2002). A pair of lateral and central gland cell masses are present on the tiny foot (Iseto and Hirose 2010). The liberated buds of *Loxomitra* swim with the ciliated tentacles or lay down their body to creep on the substratum by twisting the stalk and attaching the terminal wings to the substratum (Iseto 2002). The foot degenerates when the buds cement on the substratum and transform to the adult stage. This genus was originally created by Nielsen (1964) as a subgenus of *Loxosomella*. In *Loxomitra* sensu Nielsen (1964), the buds attach to the mother body, not by foot tip as do other *Loxosomella* species, but by the back of the stalk or the calyx. Iseto (2002) redefined the genus to include only the species having a foot with a pair of terminal wings among the species having a budding mode of *Loxomitra* sensu Nielsen (1964). This genus includes only six species and three of them, *L. mizugamaensis*, *L. ryukyuensis*, and *L. tetraorganon*, were reported from Okinawa, Japan (Iseto 2002, 2006). This genus is not commonly reported in the literature, but I assume that reports on this genus would increase worldwide if we focused more on noncommensal loxosomatids.

Loxocorone is a genus created by Iseto (2002) for the species included in the genus *Loxomitra* sensu Nielsen (1964) but excluded from *Loxomitra* sensu Iseto (2002). This genus includes species whose buds attach to the mother by the back of the stalk or the calyx but their foot is the typical *Loxosomella* type comprising the foot gland and foot groove. The genus includes two Japanese species, *L. allax* (Iseto, 2002) and *L. pseudocompressa* Konno, 1977. This genus is, however, now regarded as a junior synonym of *Loxosomella* (see Emschermann 2011; note that in this report the personal communication of the author with Iseto was in November 2009 and not in September 2002, as stated) or a subgenus of *Loxosomella* (see Nielsen 2010). The detailed study of foot groove structure (Iseto and Hirose 2010) showed that *L. allax* had similar components in the foot as *Loxosomella* (Iseto and Hirose 2010), suggesting their close relationship.

17.3.2 Some Notes on Japanese Solitary Species

It is interesting that all the solitary entoprocts reported from Japan are novel findings and have never been reported from other countries. Most loxosomatid species from other regions are also localized there with only a few species, such as *Loxomitra kefersteinii* (Claparède, 1867), *Loxosomella compressa* Nielsen and Ryland 1961, and *Loxosomella varians* Nielsen, 1964, known to have a wide distribution. The question that therefore arises is this: are loxosomatids mostly endemic animals? As of now, the answer remains unclear. The dispersal ability of solitary species is probably not greatly restricted because they can disperse not only as larvae but also as liberated buds (Ryland and Austin 1960; Sugiyama et al. 2010). Emschermann (2011) insists that distributions of cosmopolitan or widely distributed species are not appropriately evaluated but are described as 'new species' in other localities. However, he did not list any of such 'species' that could be synonymized.

The following are possible reasons for the endemic occurrence of loxosomatids: (1) most species are truly endemic, (2) faunistic surveys are insufficient to find the second and more localities, and (3) taxonomists fail to relate their local populations to one of the known species.

Solitary genera of Entoprocta have been classified based on the foot structure and budding mode. The largest genus, *Loxosomella*, is defined to have a foot with foot gland (Mortensen 1911). However, species having various types of foot gland have been included in this genus. Nielsen (1964) redefined this genus as having foot gland, foot groove, and accessory gland cells that support the foot groove. The foot gland is known to open on the underside at the position of the anterior end of the foot groove (Schmidt 1875; Iseto and Hirose 2010), which is consistent with the foot of the type species, *Loxosomella crassicauda* (Salensky, 1877). However, species that do not conform to this definition are still included in *Loxosomella*, with the genus now being apparently a mixture of multiple natural taxa. Iseto (2002) clearly distinguished *Loxomitra* from *Loxosomella*. The rest of *Loxosomella* species need to be classified into several groups. Some loxosomatids in Japan may contribute in resolving such major problems in the taxonomy of the phylum.

Loxosomella poculi Konno, 1977 is one of the species without the typical *Loxosomella* type of foot. This species has a disc-shaped foot and thus looks like *Loxosoma*, but is, nevertheless, classified in *Loxosomella* because it has a foot gland composed of several gland cells (Fig. 17.3d, e). *Loxosoma* species are known to have gland cells on the underside of the sucking disc (Iseto and Hirose 2010). The difference between *Loxosomella poculi* and *Loxosoma* species seems small: the gland cells being either aggregated or scattered. Morphological and functional investigations on the foot gland of *Loxosomella poculi* might be important in understanding the relationship of *Loxosoma* and other loxosomatids.

Loxosomella bifida Konno, 1972 walks with a pair of legs, as already mentioned. This leg structure feebly resembles the typical *Loxosomella* type (Fig. 17.3a, b). Both *L. bifida* and *Loxomitra* species have a central and a lateral pair of gland cell masses, suggesting the possibility that the laterally located legs of *L. bifida* are homologous to the terminal wings of *Loxomitra* (Iseto 2002; Iseto and Hirose, 2010).

Nielsen (2010) proposed the use of only two genera, *Loxosoma* and *Loxosomella*, in Loxosomatidae and noted that "This move will make it possible to refer species to the correct genus even when the diagnostic details of the attachment organ are undescribed." This is a practical treatment of the problematic situation. However, I consider *Loxomitra* a well-defined genus, and thus propose the use of three genera, namely, *Loxosoma*, *Loxosomella*, and *Loxomitra*. Nevertheless, it is a tentative distinction because some species do not fit into any of the three genera and need to be further studied to improve loxosomatid taxonomy.

17.3.3 Colonial Genera and Their Occurrence in Japan

Approximately 40 species of colonial entoprocts have been reported from around the world, classified into 3 families with 10 genera. Among these, 11 species from 5 genera of 2 families have been reported from Japan (Table 17.2).

Members of the genus *Barentsia* possess a muscular node at the base of the stalk. Approximately 13 species have been reported from around the world. Among these, 6 described species and 2 undescribed species have been reported from Japan (Table 17.2). *Barentsia geniculata* Harmer, 1915, reported by Toriumi (1951), was identified as *B. gracilis* by Yamada (1956). Konno (1978) reported 2 undescribed *Barentsia* species from Sado and Noto, respectively, along the Japan Sea but did not describe them in detail (Table 17.2).

The genus *Pseudopedicellina* was created by Toriumi (1951) with the description of a new species, *Pseudopedicellina mutabilis* Toriumi, 1951, from Matsushima Bay. A colony of *P. mutabilis* includes both types of individuals having a basal muscular node (*Barentsia* type) and lacking the node (*Pedicellina* type). *Pseudopedicellina* is a monotypic genus and is included in the family Barentsiidae. Konno (1971) also found *P. mutabilis* from Fukaura. Ryland (1961) also reported this species from British waters. However, Dr. Emschermann believes that the colonies represent "unhealthy conditions or crosses between species" (personal communication of Dr. Nielsen with Dr. Emschermann; see Nielsen 1989). The nature of this genus is in question. The morphological flexibility of the basal node, however, suggests the weakness of the definitions that differentiate Barentsiidae and Pedicellinidae.

The genus *Urnatella* is also included in the family Barentsiidae because the monotypic species, *U. gracilis* Leidy, 1851, has basal muscular nodes. However, they do not have a stolon as do other barentsiids, and all individuals of a colony are connected at a basal plate. All other species described as *Urnatella* (*U. dnjestriensis* Zambriborshch, 1958, *U. walkerii* Helm, 1892, *U. indica* Seshaiya, 1947) are now recognized as junior synonyms of *U. gracilis*. This species was first found in Japan on September 1974 in Saitama Prefecture (Ikeda et al. 1977) and subsequently

Table 17.2 List of colonial entoprocts found from Japan

Species	Locality	Habitat	Sexual reproduction (months)	Size (mm)	References
Barentsia benedeni (Foettinger, 1887)	Matsushima Bay	–	5–11	3–8	Toriumi (1944, 1951)
Barentsia discreta (Busk,1886)	Misaki, Miyagi Pref, Matsushima Bay, Sado Island, Muroran, Akkeshi Bay, Mukaishima, Shirahama	Attached on hydroids, bryozoans, algae, sponges, calcareous polychaete tubes, shell of mollusks, solitary ascidian, rock	6–12	4–9.5	Oka (1890, 1895), Toriumi (1949, 1951), Yamada (1956), Okada and Mawatari (1938), Honma and Kitami (1978), and Konno (1971, 1978, 1985)
Barentsia gracilis Sars, 1835	Tohoku, Hokkaido; Matsushima Bay, Akkeshi Bay, Horomoi, Mukaishima	Oyster shell, calcareous polychaete tubes, bivalve, rock	1–4	2–5	Toriumi (1951), Yamada (1956), and Konno (1971, 1985)
Barentsia hozawai Toriumi, 1949	Miyagi Pref., Japan	–	–	4	Toriumi (1949
Barentsia laxa Kirkpatrick, 1890	Matsushima Bay, Amakusa, Sado Island, Shirahama	Attached on algae, oyster shell, test of solitary ascidian, rock	9–10	4.5	Toriumi (1949, 1951), Kikuchi (1968), Honma and Kitami (1978), and Konno (1985)
Barentsia matsushimana Toriumi, 1951	Matsushima Bay, Miyagi Pref., Japan	Sponges, calcareous polychaete tubes, rock	1–4	4.5	Toriumi (1951) and Konno (1971)
Barentsia sp.	Sado	–	7	–	Konno (1978)
Barentsia sp.	Noto-Ogi	–	9	–	Konno (1978)
Loxosomatoides laevis Annandale, 1915	Matsushima Bay, Miyagi Pref., Japan	Test of solitary ascidian	–	0.7	Toriumi (1951)

(continued)

Table 17.2 (continued)

Species	Locality	Habitat	Sexual reproduction (months)	Size (mm)	References
Pedicellina choanata O'Donoghue, 1924	Akkeshi	Rock, hydroids, bryozoans, algae	–	6	Yamada (1956)
Pedicellina cernua Pallas, 1774	Miyagi Pref., Japan	Test of solitary ascidian	–		Toriumi (1949)
Pseudopedicellina mutabilis Toriumi, 1951	Matsushima Bay, Hachinohe, Asamushi, Usa	Sponges, calcareous polychaete tubes, shell of mollusks, solitary ascidian, rock	6	1.2–1.5	Toriumi (1951) and Konno (1971, 1985)
Urnatella gracilis Leidy, 1851	Kawagoe > Saitama, Lake Hachiro > Akita pref., Intake facilities at Lake Inba > Chiba Pref.	–	–		Ikeda et al. (1977), Toriumi (1977), and Oda (1982)

found in Lake Hachiro in Akita Prefecture (Toriumi 1977). The occurrence in Lake Hachiro has been repeatedly reported (Oda 1982; Ishii 1997). Oda (1982) reported the same species from Chiba Prefecture. *Urnatella gracilis* was originally found in the east of North America in 1851, and is believed to have spread worldwide anthropogenically (Emschermann 1987). It is plausible that this species might already be widely distributed across Japan.

The genus *Pedicellina* is a colonial genus that does not have a basal muscular node but has straight musculature through the stalk in each zooid. Approximately 12 species have been described from around the world. Among these, only 2 species were found in Japan, namely, *Pedicellina cernua* (Pallas, 1774) and *Pedicellina choanata* O'Donoghue, 1924. The former is a known cosmopolitan species and the latter has been reported from South Africa and Japan. *Pedicellina ichikawai* was originally described as a new species by Yamada (1956) but was synonymized with *P. choanata* by Ryland (1965) who observed the type material of *P. choanata* and compared it with the drawings of *P. ichikawai* by Yamada (1956). Both species have been reported only once each from Japan, and the survey of this genus is certainly insufficient in Japan.

The genus *Loxosomatoides* Annandale, 1908, is characterized by having strong oral calyx musculature, an oblique calyx, and an aboral shield on the calyx. Five species are currently recognized in the world and one species, *Loxosomatoides laevis* Annandale, 1915, was reported from Japan (Toriumi 1951). Toriumi (1951) originally reported this species as a new species, *L. japonicum*, but Wasson et al. (2000) synonymized it with *L. laevis* based on their revision of all the species related to the genus. Wasson et al. (2000) also postulated that *L. laevis* of Japan (Toriumi 1951) resembled that found in Chesapeake Bay half a century later and concluded that *L. laevis* found in Chesapeake Bay might have been introduced from Japan. Wood (2005) reported a new *Loxosomatoides* species, *L. sirindhornae* Wood, 2005, from Thailand. Although this species has not been reported from Japan, it is noteworthy as the second freshwater entoproct species in the world.

Coriella, *Pedicellinopsis*, *Myosoma*, *Sangavella*, and *Loxokalypus* are all colonial genera that have never been reported from Japan.

17.3.4 Some Notes on Japanese Colonial Species

Barentsia discreta (Busk, 1886) is the most widely and repeatedly reported colonial species in Japan. This species was first described by the *Challenger* expedition in Tristan Cunha and is common worldwide (summarized by Emschermann 1993 and by Wasson 1997b). This species may be the most common entoproct in Japan and sometimes occurs in the field guides of shore fauna in Japan. Their active bending movement makes their colony easy to find in the field. However, *Barentsia discreta* reported from Japan shows considerable size variations. The total length of the largest individual from Fukaura was 4 mm (Konno 1971) but the longest was 9.5 mm in Akkeshi (Yamada 1956). Such wide intraspecific variation possibly suggests the presence of cryptic species. As this species has only a few morphological characteristics, molecular data may be necessary to resolve this issue. It may be noteworthy that a specimen related to *B. discreta* is preserved in The University Museum, The University of Tokyo. This specimen is labeled as "*Ascopodaria misakiensis*," the name currently synonymized with *B. discreta*. Although the label does not contain the statement of the collector or type status, this specimen may be the type of *Ascopodaria misakiensis* Oka, 1895 because this scientific name has been used only by Oka (1895).

Barentsia benedeni (Foettinger, 1887) has been reported from different locations around the world (Europe, Atlantic and Pacific Coasts of North America, Australia, and Japan). Wasson et al. (2000) postulated the invasive nature of this species based on their findings of a recent new occurrence on the Atlantic Coast of North America. The original distribution of this species is not known, but Wasson et al. (2000) suggested the possibility of a European origin because of the presence of much older records there (Foettinger 1887). These arguments suggest that the occurrence of this species in Japan (Toriumi 1944, 1951) may also be anthropogenic, although we have no data to confirm this.

Most of the colonial species found in Japan are also found in other regions of the world. *Barentsia hozawai* Toriumi, 1949 is probably the only endemic species in Japan. This situation is different from that of the solitary entoprocts that show endemic occurrences (discussed earlier). As mentioned, some of the colonial species are believed to spread artificially and this may be one of the reasons for the extensive worldwide records. However, I have no idea if solitary species tend to be much more endemic compared to the colonial species. Evaluation of the precise distribution of colonial species seems to be an important challenge in entoproct biology. In his monograph of entoprocts in Europe, Nielsen (1989) postulated about barentsiids, writing that "many of the names appear to be synonyms and the arrangement of species in genera is somewhat haphazard" and "a thorough revision of the family is badly needed." He also postulated that further research is needed to ascertain the identities of *Pedicellina* species and to show the true distribution range. Wasson (1997b) reviewed all colonial species from the Pacific Coast of North America, revising the faunal list and the distribution range of *Barentsia* species with synonymization of some species. As such, the identification of colonial species in the original occurrence report is often unreliable, and reviews in the regions must be carried out carefully.

I summarized the occurrence records of colonial entoproct species in Japan (Table 17.2) and listed 11 species based on the literature. However, most of these records lack drawings or photographs, and none of them has preserved specimens. This situation highlights the need for taxonomic and distributional surveys with newly collected specimens in Japan.

17.3.5 Phylogeny

The position of Entoprocta in the Metazoa is still unclear. Most phylogenetic studies indicate Entoprocta is a member of the Lophotrochozoa (Dunn et al. 2008; Paps et al. 2009). However, its position within Lophotrochozoa is controversial. Mitochondrial gene organization demonstrated maximum similarity between loxosomatids and mollusks, whereas the mitochondrial protein-coding genes suggest their close relationship to Phoronida (Yokobori et al. 2008). A sister group relationship of Entoprocta with Cycliophora has recently been suggested in a number of studies (Passamaneck and Halanych 2006; Fuchs et al. 2010; Struck et al. 2014). A sister group relationship of Entoprocta + Cycliophora and Bryozoa (Ectoprocta) was also recently suggested (Hausdorf et al. 2007) Laumer et al. (2015) do not support a sister group relationship of Entoprocta with Cycliophora but suggest the closer relationship with Bryozoa. Morphological similarities between the larvae of entoprocts and basal mollusks have also been postulated (Haszprunar and Wanninger 2008; Wanninger et al. 2007), whereas Nielsen (1971, 2012) pointed to similarities in settling and metamorphosis.

Molecular studies focusing on the phylogeny within Entoprocta have been undertaken recently. Fuchs et al. (2010) indicated polyphyly of the genus *Loxosomella*. Kajihara et al. (2015) reported the paraphyletic nature of *Loxosomella*. They also demonstrated unexpected results that two *Loxosoma* species (*L. axisadversum* and *L. pectinaricola*) did not form a clade. *Loxomitra* formed a clade but appeared to be a specialized *Loxosomella*. In those phylogenetic trees, solitary species and colonial species were always separated. However, the studies did not include sequence data of Loxokalypodidae and thus could not evaluate the dichotomy between Solitaria and Coloniales.

17.4 Biological Accounts

17.4.1 Commensalism

Commensalism is a remarkable feature of solitary entoprocts. They have been found associated with various animals, such as polychaetes, sponges, bryozoans, and sipunculans (Nielsen 1964; Iseto 2005b).

In the case of polychaetes, entoprocts are often observed with tube-building polychaetes. Such association, however, shows considerable variations. Some species settle on the host body (e.g., *Loxosomella akkeshiensis* Yamada, 1956) whereas other species settle on the tube (e.g., *Loxosomella umeri* Konno, 1976) or move around in the tube (e.g., *Loxosoma monilis* Konno, 1973; *Loxosomella bifida*). This preference suggests that not only the body of the polychaete itself but the in-tube environment has benefit in their habitat selection. Also, a number of species are found on free-living polychaetes, such as *Aphrodita* and *Nephtys*, suggesting the body of polychaetes can offer sufficient habitat to some loxosomatids. The movements of loxosomatids also exhibit variation. *Loxosoma monilis* moves by alternately attaching its basal sucking disc and tentacles. *Loxosomella bifida* walks on the tube with a pair of ‘legs,’ as mentioned earlier.

In the case of sponges, loxosomatids mostly attach on the surface of the sponge and sometimes in the channel of the sponge. Only the genus *Loxosomella* has this association with sponges. Very few groups of animals are found on sponges, which usually avoid the settlement of other animals, but loxosomatids acquire tolerance against the sponge’s defensive mechanism. The foot of *Loxosomella plakorticola* Iseto and Sugiyama, 2008 firmly grabs the tissues of the sponge surface by narrowing the foot groove (Iseto et al. 2008). This attachment mode allows them to detach from the sponge under unfavorable situations. Mass detachment from the sponge is thought to occur when loxosomatids escape from predators (Sugiyama et al. 2010).

Before the studies of Iseto (2001, 2002, 2003, 2005b, 2006) from Okinawa, loxosomatids were regarded as a commensal group with a few exceptional species. Discovery of a large number of noncommensal species, however, suggested noncommensal life to be another major life mode for this animal group.

The benefits of commensalism have been discussed in several reports. Nielsen (1964) analyzed the attachment position and directions of entoprocts and concluded they are ‘energy-commensals’ that exploit the host-generated water current to efficiently obtain food particles. Emschermann (1971) postulated that avoiding sedimentation is a benefit of commensalism for loxosomatids. Iseto (2005b) indicated that noncommensal loxosomatids are threatened by predators, and the cover provided by larger animals and association with host animals might help in avoiding such risks. In summary, commensal loxosomatids may enjoy the following benefits through the relationship: (1) exploiting the host-generated water current, (2) avoiding sedimentation, (3) avoiding predators, and (4) avoiding overgrowth by other organisms. The last three benefits suggest that safety is an issue of great concern for commensal loxosomatids.

Sugiyama et al. (2010) monitored several sponges in the field and reported that the loxosomatids on sponges showed dynamic population fluctuation. They assumed predation or mass detachment to avoid predators as the reason for a sudden decrease in the population.

17.4.2 Reproduction

Both sexual and asexual reproduction is common in all solitary and colonial entoprocts. Sexual reproduction produces ciliated, trochophore-like larvae. Eggs in the female ovary are fertilized with sperm that travels through the open water. Embryos develop while attached to the mother's body by strings and swim out as fully developed larvae. The occurrence of sexual reproduction can be detected by the observation of mature gonads or developing embryos.

In Japan, detailed observations on sex differentiation were carried out by Mukai and Makioka (1980) with *Barentsia discreta*. They observed colony hermaphroditism, in which both males and females are simultaneously present in a colony. Simultaneous hermaphroditism of zooids was also reported in *Barentsia aggregata* (Johnston and Angel, 1940; Wasson, 1997a). Wasson (1997b, 1998) reported gonochorism of colonies of *Barentsia hildegardae*, indicating that the sexual mode of colonies varies among species.

An interesting feature of solitary entoprocts in Okinawa, a subtropical region, is that they rarely show sexual reproduction. Iseto et al. (2007) studied noncommensal loxosomatids annually and found that sexual reproduction occurs in a very small proportion of the individuals and is restricted to only 1 month (July or August) for several species. Sugiyama et al. (2010) also reported sexual reproduction to be rare in a sponge-inhabiting species, *Loxosomella plakorticola*, which occurred only in 16 of 2300 individuals that they observed in their 2-year survey. In these cases, sexual reproduction occurred in August, with only a single exception observed in November. Sexual reproduction is not rare in loxosomatids in mainland temperate region of Japan, and all loxosomatid species found from polychaetes have been observed to possess larvae, except *Loxosomella pseudocompressa* (Konno 1985). The only noncommensal species on the mainland, *Loxosomella shizugawaensis*, was also reported to have embryos (Konno 1985). These observations suggest that the strategies of sexual reproduction depend on climate but are independent of commensal strategies.

Sexual reproduction is also common in colonial species in mainland Japan. However, I have no data on colonial species from Okinawa.

Budding is the most common asexual mode of reproduction in all entoprocts. Surveys in Europe indicate most loxosomatids shows budding almost year round (Nielsen 1964, 1989). Iseto et al. (2007) reported budding to be active in summer in some noncommensal species in Okinawa. However, Sugiyama et al. (2010) indicated a negative correlation between the budding activity and the water temperature 2 months before. They concluded that some factor(s) related to temperature, instead of the temperature itself, affected the budding activity.

Forming hibernacula is another means of asexual reproduction found only in colonial species. It has been found in *Barentsia benedeni* (see Toriumi 1944), *B. matsushimana* Toriumi, 1951 (see Toriumi 1951; Konno 1971), and *B. gracilis* (see Konno 1971) in Japan. The latter species have two types of hibernacula: one is a vesicle at the tip of the stolon and the other is a swollen segment of the stolon (Konno 1971). The hibernacula of *B. matsushimana* are segmented, and germination occurs from segments at both ends (Emschermann 1961). Germination was reported to occur after exposure to low temperatures (Toriumi 1951; Emschermann 1961, 1982).

Colonial species often degenerate and shed their old or injured calyces. The calyces are replaced through regeneration by a process similar to budding at the stolon tip (Hyman 1951; Brien 1959). Experimental studies on regeneration were carried out with *Barentsia discreta* in Japan. Regeneration is known to occur by fragments of stalk and stolon. Stalk can regenerate a calyx both apically and basally; stolons can regenerate distally but not proximally (Mukai and Makioka 1978; Konno 1990a).

In solitary species, regeneration has been observed in only one species, *Loxosomella antarctica* Franzèn, I973 (Emschermann 1993), but not in any of the Japanese loxosomatids.

17.5 Toward a Better Understanding of the Phylum Entoprocta

As summarized in this chapter, Entoprocta has been studied actively by several Japanese zoologists. Japan may be one of the most well surveyed areas in the world for entoprocts. However, our knowledge of the phylum in Japan is still insufficient compared to other phyla. Major obstacles to the progress of entoproct biology might be insufficient faunal surveys and taxonomy. Faunal surveys provide many opportunities to discover new local occurrences and new species in Japan. There has been little focus on noncommensal species in the surveys on the mainland. Bryozoans, sipunculans, and other candidate hosts have not been surveyed by entoproct specialists in Japan. Moreover, colonial species have never been surveyed intensively by any zoologist. The number of entoproct species reported to date (=41) is apparently only a fraction of the full entoproct diversity in Japan.

References

Annandale N (1908) The fauna of brackish ponds at Port Canning, Lower Bengal. Part. VII. Further observations on the Polyzoa with the description of a new genus of Entoprocta. Rec Indian Mus 2:11–19

Annandale N (1915) Fauna of the Chilka lake. The polyzoa of the lake and of brackish water in the Gangetic delta. Mem Indian Mus 5:119–134

Brien P (1959) Classe des Endoproctes ou Kamptozoaires. In: Grasse P (ed) Traité de Zoologie, vol 5. Masson et Cie, Paris, pp 927–1007

Busk G (1886) Report on the polyzoa collected by H.M.S. *Challenger*. Report on the scientific results of the exploring voyage of H.M.S. *Challenger*. Zoology 17(3):1–47, pls. 49–10

Claparède E (1867) Miscellanées zoologiques. V. Sur le *Loxosoma kefersteini* n. sp., Bryozoaire mou du Golfe de Naples. Ann Sci Nat Zool 8(5):28–30

Cori C (1929) Kamptozoa. In: Krumbach T, Kükenthal W (eds) Handbuch der Zoologie, vol 2. Walter de Gruyter, Berlin, pp 1–64

du Bois-Reymond-Marcus E (1957) Neue Entoprocten aus der Gegend von Santos. Zool Anz 159:68–75

Dunn CW, Hejnol A, Matus DQ, Pang K, Browne WE, Smith SA, Seaver E, Rouse GW, Obst M, Edgecombe GD (2008) Broad phylogenomic sampling improves resolution of the animal tree of life. Nature (Lond) 452(7188):745–749

Emschermann P (1961) Über Brutkörper bei dem Kamptozoon *Barentsia gracilis* Sars. Zool Jb Physiol 69:333–338

Emschermann P (1969) Ein Kreislauforgan bei Kamptozoen. Z Zellforsch 97:576–607

Emschermann P (1971) *Loxomespilon perezi*—ein Entoproctenfund im Mittelatlantik. Überlegungen zur Benthosbesiedlung der Großen Meteorbank. Mar Biol 9:51–62

Emschermann P (1972) *Loxokalypus socialis* gen. et sp. nov. (Kamptozoa, Loxokalypodidae fam. nov.), ein neuer Kamptozoensystematik. Mar Biol 12:237–254

Emschermann P (1982) Les Kamptozoaires. État actuel de nos connaissances sur leur anatomie leur développement, leur biologie et leur position phylogénetique. Bull Soc Zool Fr 107:317–344

Emschermann P (1987) Creeping propagation stolons—an effective propagation system of the freshwater entoproct *Urnatella gracilis* Leidy (Barentsiidae). Arch Hydrobiol 108:439–448

Emschermann P (1993) On Antarctic Entoprocta: nematocyst-like organs in a loxosomatid, adaptive developmental strategies, host specificity, and bipolar occurrence of species. Biol Bull 184:153–185

Emschermann P (2011) New species, taxonomist's delight and faunist's plight. On the variation range in *Loxosomella vivipara* Nielsen, 1966 (Entoprocta: Loxosomatidae). Zool Meded (Leiden) 85(1):69–77

Foettinger A (1887) Sur l'anatomie des Pédicellines de la cote d'Ostende. Arch Biol 7:299–329, pl. 210

Fuchs J, Iseto T, Hirose M, Sundberg P, Obst M (2010) The first internal molecular phylogeny of the animal phylum Entoprocta (Kamptozoa). Mol Phylogenet Evol 56(1):370–379

Harmer SF (1915) Polyzoa of the Siboga Expedition. Part I. Entoprocta, Ctenostomata and Cyclostomata. Siboga Expeditie 28a:1–180, pls 181–112

Haszprunar G, Wanninger A (2008) On the fine structure of the creeping larva of *Loxosomella murmanica*: additional evidence for a clade of Kamptozoa (Entoprocta) and Mollusca. Acta Zool 89(2):137–148

Hausdorf B, Helmkampf M, Meyer A, Witek A, Herlyn H, Bruchhaus I, Hankeln T, Struck TH, Lieb B (2007) Spiralian phylogenomics supports the resurrection of Bryozoa comprising Ectoprocta and Entoprocta. Mol Biol Evol 24(12):2723–2729

Helm S (1892) *Cordylophora lacustris* and five forms of animal life. J N Y Microsc Soc 8:43–50

Hincks T (1880) A history of the British Marine Polyzoa., 2 vols. Van Voorst, London

Hincks T (1884) Contributions towards a general history of the marine Polyzoa. Ann Mag Nat Hist 13(5):356–369, pls. 313–314

Honma Y, Kitami T (1978) Fauna and Flora in the western adjacent to the Sado marine biological station, Niigata University. Ann Rep Sado Mar Biol Stat, Niigata Univ 8:7–81

Hyman LH (1951) The pseudocoelomate Bilateria–Phylum Entoprocta. In: The invertebrates: Acanthocephala, Aschelminthes, and Entoprocta. The Pseudocoelomate Bilateria, vol 3. McGraw-Hill, New York, pp 521–554

Ikeda O, Makino S, Aikawa K (1977) Appearance of fresh-water Entoprocta (Kamptozoa) *Urnatella gracilis* Leidy in Japan. Proc Jap Soc Syst Zool 13:32–38

Iseto T (2001) Three new *Loxosomella* (Entoprocta: Loxosomatidae) from coral reef shore in Okinawa, Ryukyu Archipelago, Japan. Zool Sci 18(6):879–887. doi:10.2108/Zsj.18.879

Iseto T (2002) *Loxocorone*, a new genus of the family Loxosomatidae (Entoprocta : Solitaria), with descriptions of two new *Loxomitra* (sensu stricto) and a new *Loxocorone* from Okinawa, the Ryukyu Archipelago, Japan. Zool Sci 19(3):359–367. doi:10.2108/Zsj.19.359

Iseto T (2003) Four new solitary entoprocts (Entoprocta: Loxosomatidae) from Okinawa Island, the Ryukyu Archipelago, Japan. Proc Biol Soc Wash 116(4):1007–1020

Iseto T (2005a) Where loxosomatids live? Understanding the habitat preference of loxosomatid entoprocts. Iden 59(1):15–18 [in Japanese]

Iseto T (2005b) A review of non-commensal loxosomatids: collection, culture, and taxonomy, with new implications to the benefit of commensalism (Entoprocta: Loxosomatidae). In: Moyano HI, Cancino JM, Wyse Jackson PN (eds) Bryozoan studies 2004. Taylor & Francis, London, pp 133–140

Iseto T (2006) Two new non-commensal loxosomatids (Entoprocta: Loxosomatidae) from Okinawa and Sesoko Islands, Ryukyu Archipelago, Japan. Species Divers 11(1):33–43

Iseto T, Hirose E (2010) Comparative morphology of the foot structure of four genera of loxosomatidae (Entoprocta): implications for foot functions and taxonomy. J Morphol 271 (10):1185–1196. doi:10.1002/Jmor.10863

Iseto T, Yokuta Y, Hirose E (2007) Seasonal change of species composition, abundance, and reproduction of solitary entoprocts in Okinawa Island, the Ryukyu Archipelago, Japan. Mar Biol 151(6):2099–2107

Iseto T, Sugiyama N, Hirose E (2008) A new sponge-inhabiting *Loxosomella* (Entoprocta: Loxosomatidae) from Okinawa Island, Japan, with special focus on foot structure. Zool Sci 25(11):1171–1178. doi:10.2108/Zsj.25.1171

Ishii T (1997) Sessile organisms in Lake Hachiro: *Urnatella gracilis*, a freshwater kamptozoan, and two species of freshwater bryozoans, first record occurring in Akita Prefecture. Mem Fac Educ Hum Stud Akita Univ (Nat Sci) 52:65–71

Johnston G (1847) A history of the British zoophytes, vol 1. Van Voorst, London

Kajihara H, Tomioka S, Kakui K, Iseto T (2015) Phylogenetic position of the queer, backward-bent entoproct *Loxosoma axisadversum* (Entoprocta: Solitaria: Loxosomatidae). Species Divers 20:83–88

Keferstein W (1862) Ueber *Loxosoma singulare* gen. et sp. n., den Schmarotzer einer Annelide. Z Wiss Zool 12:131–132, pl. 111

Kikuchi T (1968) Faunal list of the Zostera marina belt in Tomioka Bay, Amakusa, Kyushu. Pub Amakusa Mar Biol Lab Kyushu Univ 1:163–192

Kirkpatrick R (1890) Reports on the zoological collections made in Torres Straits by Professor A.C. Haddon, 1888–1889. Hydroida and Polyzoa. Sci Proc R Dublin Soc New Series 6:603–626

Kluge HA (1946) Kamptozoa from the Arctic Ocean. Trav Dreifuyush Arctic Expedition of the Ice-breaker “G Sedov” in the years 1937–1940. 3:149–157

Konno K (1971) On some Entoprocts found at Fukaura, Aomori Prefecture. Rep Fukaura Mar Biol 3:2–9

Konno K (1972) Studies on Japanese Entoprocta. I. On four new species of loxosomatids found at Fukaura, Aomori Prefecture. Sci Rep Hirosaki Univ 19:22–36

Konno K (1973a) Studies on Japanese Entoprocta. II. On a new species of *Loxosoma* and *Loxosomella akkesiensis* (YAMADA) from Fukaura. Sci Rep Hirosaki Univ 20:79–87

Konno K (1973b) A preliminary list of marine animals found in the vicinity of the Fukaura Marine Biological Laboratory. Rep Fukaura Mar Biol 5:2–7

Konno K (1974) Studies on Japanese Entoprocta. III. On *Loxosoma cubitus* sp. nov. from Fukaura. Sci Rep Hirosaki Univ 21:67–70

Konno K (1975) Studies on Japanese Entoprocta. V. On *Loxosomella pistilli* sp. nov. found in the tube of *Palola sciliensis* (GRUBE). Sci Rep Hirosaki Univ 22:79–81

Konno K (1976) Studies on Japanese Entoprocta. VI. Three new loxosomatids found at Fukaura. Sci Rep Hirosaki Univ 23:43–49

Konno K (1977a) Studies on Japanese Entoprocta. IV. *Loxosoma vatilli* sp. nov. and its dimorphism. Proc Jap Soc Syst Zool 13:24–31

Konno K (1977b) Studies on Japanese Entoprocta. VII. On two new species of Loxosomatidae. Sci Rep Hirosaki Univ 24:81–84

Konno K (1978) Studies on Japanese Entoprocta VIII. Survey of Japanese Kamptozoan Fauna (1). J Aomori-Ken Biol Soc 16:21–29

Konno K (1985) Studies on Japanese Entoprocta IX. Survey of Japanese Kamptozoan Fauna (2). Rep Fukaura Mar Biol 11:5–7

Konno K (1990a) Studies on Japanese Entoprocta X. Preliminary notes on the regeneration and the mode of colonization of the entoproct, *Barentsia discreta* (Busk). Rep Fukaura Mar Biol 13:16–19

Konno K (1990b) Shore fauna of Shiriuchi, Mastumae Peninsula, Hokkaido. Rep Fukaura Mar Biol 13:20–21

Laumer CE, Bekkouche N, Kerbl A, Goetz F, Neves RC, Sørensen MV, Kristensen RM, Hejnol A, Dunn CW, Girbet G, Worsaae K (2015) Spiralian phylogeny informs the evolution of microscopic lineages. Curr Biol 25(15):2000–2006

Leidy J (1851) On some American freshwater Polyzoa. Proc Acad Nat Sci Phila 5:320–322, pl. 321

Mortensen T (1911) A new species of Entoprocta, *Loxosomella antedonis*, from North-east Greenland. Medd Grønland 45(7):399–406, pl. 326

Mukai H, Makioka T (1978) Studies on the regeneration of an entoproct, *Barentsia discreta*. J Exp Zool 205:261–276

Mukai H, Makioka T (1980) Some observations on the sex differentiation of an entoproct, *Barentsia discreta* (Busk). J Exp Zool 213:45–59

Nielsen C (1964) Studies on Danish Entoprocta. Ophelia 1:1–76

Nielsen C (1971) Entoproct life-cycles and the entoproct/ectoproct relationship. Ophelia 9:209–341

Nielsen C (1989) Entoprocts, vol 41. Synopses of British Fauna (New Series). The Linnean Society of London & The Estuarine and Brackish-Water Sciences Association

Nielsen C (1996) Three new species of *Loxosoma* (Entoprocta) from Phuket, Thailand, with a review of the genus. Zool Scr 25(1):61–75

Nielsen C (2010) A review of the taxa of solitary entoprocts (Loxosomatidae). Zootaxa 2395:45–56

Nielsen C (2012) Animal evolution, 3rd edn. Oxford University Press, New Yolk

Nielsen C, Ryland JS (1961) Three new species of Entoprocta from West Norway. Sarsia 1 (1):39–45

Nitsche H (1870) Beiträge zur Kenntniss der Bryozoen. Z Wiss Zool 20:1–36, pls. 31–33

Oda S (1982) *Urnatella gracilis*, a freshwater kamptozoan, occurring in Japan. Annot Zool Jpn 55 (3):151–166

O'Donoghue CH (1924) The Bryozoa (Polyzoa) collected by the S. S. "Pickle". Rep Fish Mar Biol Surv South Afr 3(10):1–63, pls. 61–64

Oka A (1890) Entoproct polyzoa from Misaki, Japan. Doubutsugaku Zasshi 2(20):233–237

Oka A (1895) Sur la *Barentsia misakiensis*. Zool Mag 7(78):76–86, pl. 12

Okada Y, Mawatari S (1938) On the collection of Bryozoa along the coast of Wakayamaken, the middle part of Honsyu, Japan. Annot Zool Jpn 17:445–462, pl. 424

Pallas PS (1774) Spicilegia zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur, vol 1(10)

Paps J, Baguñà J, Riutort M (2009) Lophotrochozoa internal phylogeny: new insights from an up-to-date analysis of nuclear ribosomal genes. Proc R Soc Lond B Biol Sci 276:1245–1254. doi:10.1098/rspb.2008.1574

Passamaneck Y, Halanych KM (2006) Lophotrochozoan phylogeny assessed with LSU and SSU data: evidence of lophophorate polyphyly. Mol Phylogenet Evol 40(1):20–28

Robertson A (1900) Studies in Pacific Coast Entoprocta. Proc Calif Acad Sci 2(3):323–348, pl. 316

Ryland JS (1961) The occurrence of *Pseudopedicellina mutabilis* Toriumi (Entoprocta) in British waters, with a note on *Pedicellina nutans* Dalyell. Ann Mag Nat Hist 13(3):377–383

Ryland JS (1965) Some New Zealand Pedicellinidae (Entoprocta), and a species new to Europe. Trans R Soc N Z Zool 6(19):189–205

Ryland JS, Austin AP (1960) Three species of Kamptozoa new to Britain. Proc Zool Soc Lond 133:423–433

Salensky M (1877) Etudes sur les Bryozoaires Entoproctes. Ann Sci Nat Zool Ser 6 5(3):1–60, pls.12–15

Salvini-Plawen LV (1968) Neue Formen im marinen Mesopsammon: Kamptozoa und Aculifera. Ann Naturhist Mus Wien 72:231–272, pls. 231–239

Sars M (1835) Beskrivelser og iagttagelser over nogle mærkelige eller nye i havet ved den bergenske kyst levende dyr af polypernes, acalephernes, radiaternes, annelidernes, og molluskernes classer. Thorstein Hallager, Bergen

Schmidt O (1875) Die Gattung *Loxosoma*. Arch Mikr Anat 12:1–14, 13 plates

Seshaiya RV (1947) On *Urnatella indica* Seshaiya, a freshwater entoproctan from South India. Rec Indian Mus 45(4):283–289

Struck TH, Wey-Fabrizius AR, Golombek A, Hering L, Weigert A, Bleidorn C, Klebow S, Iakovenko N, Hausdorf B, Petersen M, Kuck P, Herlyn H, Hankeln T (2014) Platyzoan paraphyly based on phylogenomic data supports a noncoelomate ancestry of spiralia. Mol Biol Evol 31(7):1833–1849

Sugiyama N, Iseto T, Hirose M, Hirose E (2010) Reproduction and population dynamics of the solitary entoproct *Loxosomella plakorticola* inhabiting a demosponge, *Plakortis* sp. Mar Ecol Prog Ser 415:73–82. doi:10.3354/meps08747

Toriumi M (1944) Brackish-water Bryozoa (in Japanese). Zool Mag 56:20–25

Toriumi M (1949) On some Entoprocta from Japan. Sci Rep Tohoku Univ 4th Ser (Biol) 18:223–227

Toriumi M (1951) Some entoprocts found in Matsushima Bay. Sci Rep Tohoku Univ 4th Ser (Biol) 19:17–22

Toriumi M (1977) Invertebrates in the regulating reservoir of Lake Hachiro. Rep. Res. Group of the fauna in the regulating reservoir of Lake Hachiro, Sendai

Wanninger A, Fuchs J, Haszprunar G (2007) Anatomy of the serotonergic nervous system of an entoproct creeping-type larva and its phylogenetic implications. Invertebr Biol 126 (3):268–278

Wasson K (1997a) Systematic revision of colonial kamptozoans (entoprocts) of the Pacific Coast of North America. Zool J Linn Soc 121(1):1–63

Wasson K (1997b) Sexual modes in the colonial kamptozoan genus *Barentsia*. Biol Bull 193:163–170

Wasson K (1998) Sexual reproduction in the colonial kamptozoan *Barentsia hildegardae*. Invertebr Biol 117(2):123–128

Wasson K (2002) A review of the invertebrate phylum Kamptozoa (Entoprocta) and synopsis of kamptozoan diversity in Australia and New Zealand. Trans R Soc S Aust 126(1):1–20

Wasson K, Holle BV, Toft J, Ruiz G (2000) Detecting invasions of marine organisms: kamptozoan case histories. Biol Invasions 2:59–74

Wood TS (2005) *Loxosomatoides sirindhornae*, new species, a freshwater kamptozoan from Thailand (Entoprocta). Hydrobiologia 544(1):27–31

Yamada M (1956) The fauna of Akkeshi Bay XXIV. Entoprocta. J Fac Sci Hokkaido Univ Ser VI Zool 2(3):237–243

Yokobori S, Iseto T, Asakawa S, Sasaki T, Shimizu N, Yamagishi A, Oshima T, Hirose E (2008) Complete nucleotide sequences of mitochondrial genomes of two solitary entoprocts, *Loxocorone allax* and *Loxosomella aloxiata*: implications for lophotrochozoan phylogeny. Mol Phylogenet Evol 47(2):612–628

Zambriborshch FS (1958) Representative of an invertebrate class–Kamptozoa–new for the fresh waters of the USSR (*Urnatella dnjestriensis*, sp. n.). Zool Zh 37(11):1741–1743

Chapter 18
Some Comments on the Taxonomy of the Peanut Worms (Annelida: Sipuncula) in Japanese Waters Toward a Future Revision

Teruaki Nishikawa

Abstract The history of Japanese sipunculan taxonomy is briefly reviewed here. Some possible examples of cryptic speciation are also given for sipunculans with wide geographic distribution and records far from Japanese waters, as strongly suggested by recent molecular phylogenetic analyses: these include Japanese populations referred to as *Sipunculus nudus*, *Siphonosoma cumanense*, *Themiste hexadactyla*, *Antillesoma antillarum*, *Aspidosiphon laevis*, and *Phascolosoma perlucens*. Future taxonomic revisions of these species, which may be inevitable, would further our understanding of sipunculan diversity in Japanese waters. Reference to *Siphonosoma australe takatsukii*, recently recorded from the Ryukyu Islands, is also made.

Keywords Sipunculans • Taxonomy • Morphology • Molecular phylogenetics • Cosmopolitan • Circumtropical • Japan

18.1 Introduction

Taxonomy has been greatly affected by recent remarkable advances in molecular phylogeny and this doubtlessly holds true for sipunculans (‘hoshimushi’ in Japanese, meaning ‘star worms,’ probably derived from the German equivalent, Sternwürmer; see Fig. 18.1). Such changes generally have been, and will be, much benefitted by well-organized morphology-based taxonomy, as exemplified by the late Prof. Edward B. Cutler’s magnum opus (Cutler 1994). This monograph revealed the then known occurrences of 161 valid species or subspecies in 17 genera and 6 families worldwide, including many cosmopolitan species and geographically

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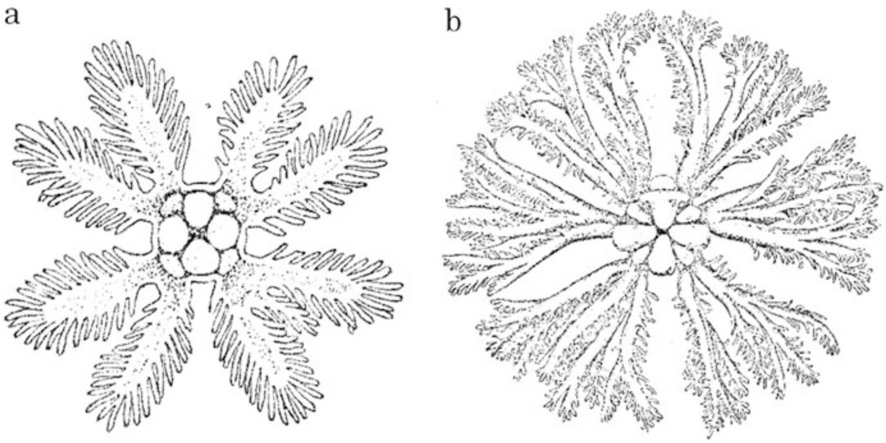

Fig. 18.1 Frontal views of tentacular crown of *Themiste blanda* with four stems (**a**) and *T. hexadactyla* with six stems (**b**), drawn from Japanese specimens, cited from Text-Figs. 10 and 13, respectively, of Satô (1930). Scales are different between **a** and **b**

widespread species consequent to morphological similarities among populations and consequent taxonomic lumping. The lumping seems to have been supported by the knowledge that some sipunculans have larvae with a long pelagic duration, even for several months (for details and criticism, see Schulze et al. 2012). More recently, cryptic speciation has been detected among some of these cosmopolitan species by Du et al. (2009), Kawauchi and Giribet (2010), Schulze et al. (2012), Kawauchi et al. (2012), Hsu et al. (2013), and Kawauchi and Giribet (2014). Molecular phylogeny has also revealed polyphyly or paraphyly in some genera in Cutler's (1994) system (Schulze et al. 2007; Kawauchi et al. 2012), but his traditional generic system is retained in the present review in hope of future revisions. However, the new six-family system of Kawauchi et al. (2012) is adopted here.

The Japanese sipunculan fauna was reviewed by Nishikawa (1992) using Cutler's (1994) system, and about 50 species in 14 genera were recognized based on work by Cutler and Cutler (1981) and Cutler et al. (1983, 1984). Nishikawa's (1992) review, however, should be thoroughly reexamined using molecular techniques in the future, which will result in nomenclatural changes (often accompanied by recoveries of once invalidated species names) and provide our better understanding of species delimitation, speciation, phylogeny, and conservation. Presented here are some notes and comments on only a few species as examples of such possible reexaminations.

18.2 Brief History of Sipunculan Taxonomy in Japan

Dr. Iwaji Ikeda was the first Japanese taxonomist of sipunculans in the sense of modern taxonomy, studying at, and then working as a lecturer for, the College of Science, Tokyo Imperial University. He later moved to Hiroshima Higher Normal

School (a predecessor of the present Hiroshima University) as a full professor, then to Kyoto Imperial University (a predecessor of the present Kyoto University) until his death. A part of his collection is still available at the University Museum, University of Tokyo (see Nishikawa and Ueshima 2006), including some of the specimens described by Ikeda (1904, 1905) but lacking the material in Ikeda's (1924) paper. The second sipunculan taxonomist was Dr. Hayao Satô of the Tohoku Imperial University, whose collection is kept in the Tohoku University Museum (for his name-bearing type specimens and their taxonomy, see Cutler and Cutler 1981). Satô (1939) published a monograph of the Japanese sipunculans (and echiurans) as his final work. It seems that Dr. Satô had no direct contact with Prof. Ikeda, who passed away in 1922 at the age of 51, whereas Satô published his first sipunculan paper in 1930, which included acknowledgments to many senior taxonomists but did not mention Ikeda (Satô 1930).

After about 40 years of non-activity, Edward B. and Norma J. Cutler conducted comprehensive studies of the Japanese sipunculans, using a large number of specimens newly collected both by themselves and many modern Japanese marine biologists, and also examined the collections of Ikeda and Satô. Their intensive energetic efforts resulted in Cutler and Cutler (1981) and Cutler et al. (1983), (1984). Their stay in Japan in 1979 was hosted by the noted polychaete taxonomist, Dr. Minoru Imajima of the National Science Museum, Tokyo (a predecessor of the National Museum of Nature and Science, Tsukuba), and I also aided their activities in a limited fashion.

18.3 Some Comments on Japanese Sipunculan Taxonomy

Only a few species are shown here as examples as their taxonomy will likely be revised by a combination of molecular and morphological analyses. They are discussed in the familial order used by Kawauchi et al. (2012).

18.3.1 "Sipunculus nudus" *(Japanese Name: suji-hoshimushi)*

This species is peculiar among Japanese sipunculans in that the trunk surface has an iridescently shiny appearance and is divided markedly into numerous rectangular or square areas. Such an external appearance is reminiscent of a kind of braid ('himo' in Japanese) made from bundles of silk thread to tie the front halves of a Japanese formal kimono coat called a 'haori.' Old literature of natural history written probably around Nagoya in the late Edo period (early to middle of the nineteenth century) finds a marine worm called 'haori-no-himo' with drawings, which may safely refer to this species; this name remains, however, completely forgotten in modern taxonomy since the Meiji era (for details, see Nishikawa 2001). In Japanese waters the species has so far been recorded from Mutsu Bay in the north to the Ryukyus in the south, but never from the Sea of Japan. Currently, the population density seems to have markedly decreased at previous localities north of the Ryukyu Islands and is categorized as “near threatened” (Nishikawa 2012a). This finding contrasts with probable high densities in the 1930s, when a huge number of worms were commercially collected for fish bait in Ise Bay (near Nagoya), the Seto Inland Sea, and northern Kyushu (Nishikawa 2007).

Sipunculus nudus Linnaeus, 1767 was established with “Habitat in Oceano Europaeo” (Linnaeus 1767), and is included in the family Sipunculidae in Kawauchi et al. (2012). This species has been said to be “found in temperate, subtropical and tropical waters in all oceans” (Cutler 1994). However, recent molecular studies have revealed its cryptic speciation (Hsu et al. 2013; Kawauchi and Giribet 2014). Kawauchi and Giribet (2014), using nuclear 28S rRNA and H3, and mitochondrial 16S rRNA and COI genes, found at least six distinct clades, one of which is composed of samples from France and Spain and safely referable to *S. nudus* sensu stricto, and another clade (with two subclades) constituting samples from China (cited from a public database; the Jinjian data excluded) and Vietnam. On the other hand, Hsu et al. (2013) recognized four clades based on partial sequences of the COI gene in the samples collected along southern Chinese coasts; one of the clades, composed of samples from Jinjian, was obscurely clustered with a group including even French samples.

According to our preliminary molecular analysis using the partial sequences of the COI gene (Kusuyama et al., unpublished data), all the newly sequenced samples from Japanese localities, including the Ryukyu Islands, did not belong to any clades defined by Hsu et al. (2013) and Kawauchi and Giribet (2014). Most of the Japanese samples seem to be rather closely related to samples from Jinjian. Very complicated patterns and processes of evolution may have been possible in this species in the Far East. Further detailed analyses are necessary for our better understanding of the Japanese ‘suji-hoshimushi.’

18.3.2 “Siphonosoma cumanense” *(Japanese Name: suji-hoshimushi-modoki)*

Siphonosoma cumanense (Keferstein, 1867), now considered in the family Siphonosomatidae in the new system of Kawauchi et al. (2012), has been recorded in tropical and subtropical waters from the western Atlantic, the Pacific, and the Indian Oceans, as well as the Red Sea (Cutler 1994). In Japan this species has been found from Mutsu Bay in the north to the Ryukyu Islands in the south, occurring both on the coasts of the Pacific (including the Seto Inland Sea) and the Sea of Japan. The population density in Japan seems to be generally decreasing, although to a lesser extent than *S. nudus* (see above) and is categorized as “near threatened” (Nishikawa 2012b), in comparison with the 1930s when a huge number of worms were commercially collected for fish bait in Ise Bay, the Seto Inland Sea, and the northern Kyushu Island (Nishikawa 2007).

Kawauchi et al. (2012) made an extensive molecular phylogenetic analysis of sipunculans using 16S rRNA, 18S rRNA, 28S rRNA, H3, H4, and COI genes, and revealed a considerable difference between West Atlantic and New Caledonian samples referred to *S. cumanense*. According to our preliminary molecular analysis using the partial COI gene (Kusuyama et al., unpublished data), the newly sequenced Japanese samples were markedly distinct from the Atlantic ones cited from the DNA database (DDBJ/EMBL/GenBank); as the New Caledonian sample lacked COI information, it could not be included in our analysis. As the type locality of *S. cumanense* is Cumana, Venezuela in the West Atlantic, the Japanese population will probably be described as a separate species. Further detailed analyses are in progress.

18.3.3 “Themiste hexadactyla” *(Japanese Name: mutsude-hoshimushi)*

The Japanese sipunculans belonging to the subgenus *Themiste* of the genus *Themiste* (newly positioned in the family Golfingidae in the Kawauchi et al. (2012) system) have been identified as *Themiste blanda* (Selenka and De Man in Selenka 1883) with four primary tentacular stems (Fig. 18.1a), or *T. hexadactyla* (Satô, 1930) with six stems (Fig. 18.1b). *Themiste blanda* was established for the specimens from “Japan” and “Enosima” in Sagami Bay, and has been recorded from Honshu and Hokkaido, Japan (Cutler 1994), as well as the Sea of Okhotsk, Russian Coast of the Sea of Japan, and Jeju Island, Korea (Maiorova and Adrianov 2013); this species has no molecular data.

The six-stemmed *Themiste hexadactyla* was established by Satô (1930) for the specimens collected intertidally or subtidally from Mutsu Bay, northern Japan. This species was long regarded as a junior synonym of *T. pyroides* (Chamberlin, 1920) with six stems, and therefore *T. pyroides* was regarded to exhibit a so-called amphi-Pacific pattern of geographic distribution (see Cutler 1994; but also see Maiorova and Adrianov 2013). Recently, however, the Vostok Bay population in the Sea of Japan has been shown to show a markedly different pattern of development from the population in British Columbia by Adrianov et al. (2008). Further, molecular phylogenetic studies using mitochondrial COI and 16S rRNA genes by Schulze et al. (2012) showed a possible genetic differentiation between the Vladivostok and the Vancouver populations. Therefore, I agree with the conclusion of Maiorova and Adrianov (2013) that *T. hexadactyla* is valid. Embryological and molecular data are expected newly from the Japanese population to compare this and the Russian one.

18.3.4 “Antillesoma antillarum” *(Japanese Name: anchira-samehada-hoshimushi),* “Aspidosiphon laevis” *(kado-tate-hoshimushi), and “Phascolosoma perlucens” (magari-samehada-hoshimushi)*

Antillesoma antillarum (Grübe and Oersted, 1858), with the type locality in the West Indies, newly positioned in the family Antillesomatidae in Kawauchi et al.’s (2012) system, has been regarded as “a cosmopolitan species found in tropical and subtropical” waters with many junior synonyms (Cutler 1994). In Japanese waters it has been recorded from the Kii Peninsula, the Seto Inland Sea, off Kyushu Island, and the Ryukyu Islands (Nishikawa 2007). This species has usually two pairs of retractor muscles, but sometimes only a single pair has been observed because of fusion of the two muscles on each side, and for such ‘abnormal’ individuals *P. onomichianum* (Ikeda, 1904) was once established. The molecular analysis by Kawauchi et al. (2012) molecular analysis may show a certain genetic differentiation between samples from Thailand (Indian Ocean) and the Barbados (West Atlantic).

Aspidosiphon (*Paraspidosiphon*) *laevis* Quatrefeges, 1865 in the family Aspidosiphonidae has a cosmopolitan circumtropical distribution (Cutler 1994) with the type locality in the Indian Ocean (Saiz Salinas 1984). It has been rarely recorded in Japanese waters from Katsuyori (as *A. angulatus* Ikeda, 1904) and Kasari Bay (Nishikawa 2007), Amami Ōhshima Island. The analysis by Kawauchi et al. (2012) shows a remarkable genetic differentiation between New Caledonian and West Pacific samples, and therefore it may be possible that the Japanese population be called otherwise.

The molecular analysis of Kawauchi and Giribet (2010) has proved that a circumtropical *Phascolosoma perlucens* Baird, 1868 species complex, in the family Phascolosomatidae, is composed of four distinct lineages. The Japanese population previously referred to as *P. perlucens* (Japanese name: magari-samehada-hoshimushi) has not yet been analyzed molecularly, but the specimens from Thailand constituted one of those lineages. As the type locality of *P. perlucens* is Jamaica, the Japanese population will be called otherwise; one of its junior synonyms may possibly be recovered.

In these three species complexes, comprehensive molecular analyses of Japanese samples should add greatly to a better understanding of Japanese (and global) sipunculan fauna.

18.4 Recent Additions to Japanese Sipunculan Fauna

Siphonosoma australe takatsukii Satô, 1935 was established as the binomen *Siphonosoma takatsukii* for a specimen from Yap Island, but later treated as a subspecies of *S. australe* Keferstein, 1865 by Cutler and Cutler (1981). At that time

S. pescadolense Satô, 1939, established for a specimen from Penghu Is., Formosa, was also synonymized with *S. autrale takatsukii*. Thus, this subspecies remained to be represented only by two specimens, one from Yap and the other from Formosa. To this time it has been collected from Amami Ōshima Island, Okinawa Island, and Ishigaki Island (Nishikawa 2007).

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References

Adrianov AV, Maiorova AS, Malakhov VV (2008) Embryonic and larval development of the peanut worm *Themiste pyroides* (Sipuncula: Sipunculoidea) from the Sea of Japan. Invertebr Reprod Dev 52:143–151

Cutler EB (1994) The Sipuncula: their systematics, biology, and evolution. Comstock Publishing Associates, Ithaca

Cutler EB, Cutler NJ (1981) A reconsideration of Sipuncula named by I. Ikeda and H. Sato. Publ Seto Mar Biol Lab 26:51–93

Cutler ER, Cutler NJ, Nishikawa T (1983) *Siphonosoma cumanense* and *S. edule* (Sipuncula): a reevaluation of their different status. Publ Seto Mar Biol Lab 27:265–267

Cutler ER, Cutler NJ, Nishikawa T (1984) The Sipuncula of Japan: their systematics and distribution. Publ Seto Mar Biol Lab 29:249–322

Du XD, Chen Z, Deng YW, Wang QH (2009) Comparative analysis of genetic diversity and population structure of *Sipunculus nudus* as revealed by mitochondrial *COI* sequences. Biochem Genet 47:884–891

Hsu TH, Ning Y, Gwo JC, Zeng ZN (2013) DNA barcoding reveals cryptic diversity in the peanut worm *Sipunculus nudus*. Mol Ecol Resour 13:596–606

Ikeda I (1904) The Gephyrea of Japan. J Coll Sci Imp Univ Tokyo 20(4):1–87

Ikeda I (1905) Gephyreans collected by Professor Dean at Manjuyodi, Southern Negros (Philippine Is.). Annot Zool Jpn 5:169–174

Ikeda I (1924) Further notes on the Gephyrea of Japan, with descriptions of some new species from the Marshall, Caroline and Palau Islands. Jpn J Zool 1(2):23–44

Kawauchi GY, Giribet G (2010) Are there true cosmopolitan sipunculan worms? A genetic variation study within *Phascolosoma perlucens* (Sipuncula, Phascolosomatidae). Mar Biol 157:1417–1431

Kawauchi GY, Giribet G (2014) *Sipunculus nudus* Linnaeus, 1766 (Sipuncula): cosmopolitan or a group of pseudo-cryptic species? An integrated molecular and morphological approach. Mar Ecol 35:478–491

Kawauchi GY, Sharma PP, Giribet G (2012) Sipunculan phylogeny based on six genes, with a new classification and the descriptions of two new families. Zool Scr 41:186–210

Linnaeus C (1767) Systema naturae, vol 1, part 2, 12th edn. Laurentius Salvius, Stockholm

Maiorova AS, Adrianov AV (2013) Peanut worms of the phylum Sipuncula from the Sea of Japan with a key to species. Deep-Sea Res II 86–87:140–147

Nishikawa T (1992) Phylum Sipuncula. In: Nishimura S (ed) Guide to seashore animals of Japan with color pictures and keys, vol 1. Hoiku-sha, Osaka, pp 299–305

Nishikawa T (2001) Ito Keisuke and his zoology. In: Anonymous (ed) A pioneer in natural science bridging Edo and Meiji periods. Memorial symposium for Ito Keisuke's 100th anniversary after his death, Nagoya University, Nagoya, pp 17–19 www.nul.nagoya-u.ac.jp/event/sympo/sympo.pdf

Nishikawa T (2007) Phylum Sipuncula. In: Iijima A (ed) Report of the 7th national survey on the natural environments: shallow sea survey (tidal flats). Biodiversity Center of Japan, Nature Conservation Bureau, Ministry of the Environment, Fujiyoshida, pp 172–176

Nishikawa T (2012a) *Sipunculus nudus*. In: Japanese Association of Benthology (ed) Threatened animals of Japanese tidal flats: red data book of seashore benthos. Tokai University Press, Hadano, p 234

Nishikawa T (2012b) *Siponocoma cumanense*. In: Japanese Association of Benthology (ed) Threatened animals of Japanese tidal flats: red data book of seashore benthos. Tokai University Press, Hadano, p 234

Nishikawa T, Ueshima R (2006) A list of the sipunculan collection of the Department of Zoology, the University Museum, the University of Tokyo. In: Ueshima R (ed) Catalogue of invertebrate collection deposited in the Department of Zoology, the University Museum, the University of Tokyo, part 1. Mater Rep Univ Mus Univ Tokyo 62:1–13

Saiz Salinas JI (1984) Los tipos de sipunculidos de de Quatrafages del Museo de Paris. Servicio Editorial de la Universidad del Pais Vasco/Euskal Herriko Unibertsitateko Argitarapen-Zerbitzua, Bilbao

Satô H (1930) Report of the biological survey of Mutsu Bay. 15. Sipunculoidea. Sci Rep Tôhoku Imp Univ 4th Ser Biol 5:1–40

Satô H (1939) Studies on the Echiuroidea, Sipunculoidea and Priapuloidea of Japan. Sci Rep Tôhoku Imp Univ 4th Ser Biol 14:339–460

Schulze A, Cutler EB, Giribet G (2007) Phylogeny of sipunculan worms: a combined analysis of four gene regions and morphology. Mol Phylogenet Evol 42:171–192

Schulze A, Maiorova A, Timm LE, Rice ME (2012) Sipunculan larvae and "cosmopolitan" species. Integr Comp Biol 52:497–510

Selenka E (1883) Die Sipunculiden: eine systematische monograph, specieller Theil, Beschreibung der Gattungen und Arten. In: Anonymous (ed) Reisen im Archipel der Philippinen von Dr. C Semper, part 2, Wissenschaftliche Resultate, vol 4. C.W. Kreidel, Wiesbaden, pp 3–131

Chapter 19
Nereididae (Annelida) in Japan, with Special Reference to Life-History Differentiation Among Estuarine Species

Masanori Sato

Abstract The Japanese fauna of Nereididae, which is the most successful annelid family in estuarine low-salinity and freshwater habitats, is reviewed here. A list of all nereidid species so far recorded from Japan (54 species belonging to 20 genera) is presented, with the information of type locality and distributional range in and around Japan for each species. Current topics on the estuarine nereidid fauna, consisting of 15 species, are the focus. The life-history modes of 4 species belonging to 2 genera (3 in *Hediste* and 1 in *Tylorrhynchus*) are compared. As do many marine nereidids, 2 of these *Hediste* and 1 *Tylorrhynchus* species show reproductive swarming preceded by epitokous metamorphosis. In these 3 species, however, the epitoky differs more or less from that into the common heteronereis form, which is almost uniform throughout the family.

The adaptive and evolutionary significance of their unique epitoky are discussed in relation to their life-history characteristics in Asian estuaries. Some of the Japanese estuarine nereidids are in danger of extinction for reasons of severe habitat loss by recent anthropogenic land reclamation.

Keywords Epitokous metamorphosis • Estuary • *Hediste* • Life cycle • Polychaete Reproductive swarming • *Tylorrhynchus*

19.1 Introduction

Polychaetes dominate marine and estuarine macrobenthic communities in a wide range of habitats in all depths, with a few species occurring in freshwaters (Dales 1963; Beesley et al. 2000; Barnes et al. 2001). Thus, polychaetes are ecologically among the most important animals in marine and estuarine habitats (Beesley et al. 2000). They have various feeding modes, with a major role in the breakdown,

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subduction, and incorporation of organic matter into sediments and their aeration (e.g., Scaps 2002). Also, they are critical in marine and estuarine food chains, as important prey for various carnivores such as fishes (Kan et al. 2016) and wading birds (Iwamatsu et al. 2007), and as predators in their own right (Imabayashi et al. 1996). Some species are commercially used as fishing bait (Okuda 1933; Saito et al. 2011, 2014), and some species cause economic damage as serious fouling organisms or as pests of commercial shellfish (Sato-Ohkoshi et al. 2015).

Polychaetes vary greatly in form, ranging in size as adults from less than a millimeter, as in some interstitial species, to well over 3 m in length (e.g., some eunicids), with their lives spanning from a few weeks to several years (Beesley et al. 2000). In Japan, the largest body size of polychaetes was recorded from a specimen of *Eunice aphroditois* [Japanese name: oni-isome] (Eunicidae) collected from Shirahama, Wakayama Prefecture, which was measured as 299 cm in body length in life (120 cm after fixation in 10 % formalin seawater), 25 mm in maximum body width (excluding parapodia) in life, and 673 in total number of chaetigers (Uchida et al. 2009).

Rouse and Pleijel (2001) estimated that the current number of accepted polychaete species is around 9000. According to Miura (2000), these are classified into 89 families in 26 orders. Recent molecular phylogenetic studies suggested that Polychaeta is a non-monophyletic group within Annelida: another annelid class, Clitellata (oligochaetes and leeches), and two traditional non-annelid phyla (Echiura and Sipuncula) are included in a clade together with many polychaete families in the annelid phylogenetic trees reconstructed by recent molecular studies (Struck et al. 2011).

Japan is now known to be located within a hotspot area with the highest richness of marine species extending from Asia to Australia in the Western Pacific (Fujikura et al. 2010; Tittensor et al. 2010). The first report on the Japanese polychaete fauna was made by an Austrian taxonomist, Marenzeller (1879), who described 30 species including 24 new species, followed by reports by himself and several other European and American specialists (see Imajima 2005). Parts of their materials were supplied by expeditions to Japan (e.g., voyages of the vessels *Challenger* and *Albatross*). At the same time and later, three Japanese authorities, namely, Akira Izuka (see his publication list by Nishi and Tanaka 2011), Shiro Okuda, and Minoru Imajima (see Imajima 2005), have described many polychaete species from Japan, as great contributions to constructing the basic knowledge of the Japanese polychaete fauna. At present, several younger taxonomists continue to find additional species new to Japanese fauna or new to science and to reexamine some known species to clarify the entire Japanese fauna.

According to Imajima (2005), 930 species of polychaetes are currently recorded from Japan. This total species number is comparable to those in Australia (1139 species; Beesley et al. 2000). Undoubtedly, many more unknown species await our description particularly in southern Japan with subtropical coral islands, and in the deep bottom layers around Japan, where previous surveys have been limited.

Here, current knowledge of taxonomy on the Japanese species of Nereididae, particularly on the estuarine species, is reviewed. This annelid family is probably the most familiar to us, because nereidids are commonly found around our human lives, such as in the land–sea interface, and some are most successful in estuarine low-salinity and freshwater habitats. Of a total of 197 species (representing 78 genera in 26 families) known as nonmarine polychaetes in the world, 61 belong to Nereididae (Glasby et al. 2009). It is noticable that highly variable life-history characteristics are found among relatively few estuarine species.

19.2 General Characteristics of Nereididae

19.2.1 Morphology

The following description is mainly based on Imajima (1972, 1996), Beesley et al. (2000), and Rouse and Pleijel (2001).

The prostomium usually has a dorsal pair of antennae and a ventral pair of large biarticulated palps at the anterior margin. Two pairs of eyes are usually present in the prostomium. The peristomium and the first segment are fused and carry usually four pairs of tentacular cirri. The muscular eversible pharynx constitutes the proboscis, which is divided into an outer (maxillary) and inner (oral) ring, with a pair of laterally situated jaws at the distal end (as seen on the everted proboscis). The rings usually have a number of chitinous paragnaths (often conical, sometimes bar-like or comb-like) or fleshy papillae, arranged in species-specific regular patterns.

Parapodia consist of a notopodium and a neuropodium, each of which is usually composed of several flattened lobes and a cirrus (dorsal or ventral cirrus, respectively) and mostly supported by an acicula (notoacicula or neuroacicula, respectively), referred to as ‘biramous.’ In most genera, parapodia are biramous, except the first two pairs, which are sub-biramous, having an ordinary neuropodium and a reduced notopodium consisting of the dorsal cirrus and a single lobe with or without a notoacicula. In Namanereinae, including two genera, *Namanereis* and *Namalycastis*, all parapodia are sub-biramous throughout.

Both noto- and neurochaetae are generally compound (additional simple chaetae occur in some taxa), usually including homo-, sesqui-, or heterogomph spinigers and falcigers (Fig. 19.1).

19.2.2 Species Diversity

According to Beesley et al. (2000), Nereididae includes at least 39 genera and 535 species in the world. From Japan, 54 species belonging to 20 genera are currently reported. In Table 19.1, all the Japanese nereidids are listed with taxonomic notes such as synonym, type locality, and distributional range in and around

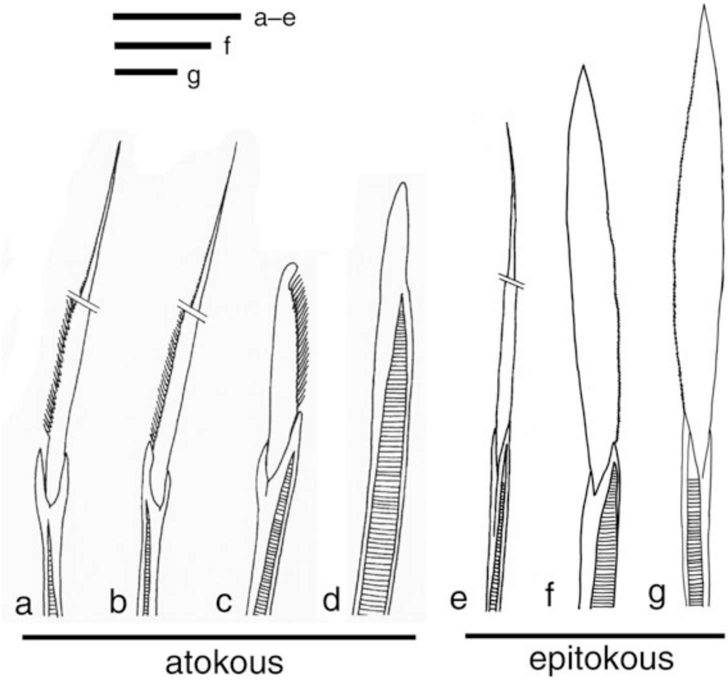

Fig. 19.1 Representative atokous (**a**–**d**) and epitokous (**e**–**g**) chaetae of nereidid polychaetes. (**a**–**e**) Chaetae of *Hediste diadroma*. (After Sato 2004): (**a**) homogomph* spiniger; (**b**) heterogomph** spiniger; (**c**) heterogomph falciger; (**d**) simple chaeta; (**e**) epitoke-specific sesquigomph*** spiniger; (**f**) paddle-like natatory chaeta of *Tylorrhynchus osawai* (unpublished data from an epitokous male collected from Yuriage, Natori-shi, Miyagi Prefecture on 20 October, 1979); (**g**) paddle-like natatory chaeta of the typical heteronereis epitokes in *Nectoneanthes uchiwa*. (After Sato 2013). *Bars* 0.05 mm. (*) with symmetrical articulation at a right angle to the long axis of the shaft; (**) with asymmetrical articulation oblique to the long axis of the shaft; (***) with asymmetrical articulation nearly at a right angle to the long axis of the shaft

Japan. At least 10 more species have been found from southern Japan as new to Japanese fauna (Sato et al., unpublished data). The species diversity of Nereididae in Japan is comparable to that in China (81 species belonging to 19 genera; Wu et al. 1985) and in Australia (70 species belonging to 17 genera; Beesley et al. 2000), and slightly higher than that in Korea (33 species belonging to 13 genera; Paik 1989).

19.2.3 Reproduction

Sexes are usually separate (dioecious). Reproductive and developmental modes of nereidids are conspicuously variable even among morphologically similar congeneric species (Sato 1999), although all nereidids are semelparous (breeding only once during the lifetime) (Olive 1983).

Table 19.1 List of nereidid species reported from Japan: 54 species belonging to 20 genera have been recorded

Subfamily genus	Name of species (synonym)	Type locality	Distribution in Japan and (neighboring countries)	"Japanese name," habitats, and remarks[a]	References
Namanereidinae					
Namanereis	*N. littoralis* (Grube) species group (=*Lycastopsis augeneri* Okuda, 1937)	Brazil	Hokkaido to middle Honshu (Russian Far East, Korea, Yellow Sea)	"Oiwake-gokai," upper intertidal	Imajima (1972, 1996), Wu et al. (1985), Paik (1989), and Glasby (1999), and Nishi (2003)
Namalycastis	*N. hawaiiensis* (Johnson, 1903)	Hawai	Southern Kyushu, Ryukyu Arc	Estuaries or freshwaters, widespread in tropic western Pacific	Glasby (1999) and Sato (unpublished data)
Gymnonereidinae					
Ceratocephala	*Ceratocephala borealis* Wesenberg-Lund, 1950	Greenland	Off Sanriku, eastern coast of northern Honshu	"Kita-gokai," 248–1498 m deep	Imajima (2009, 2015)
Tambalagamia	*T. fauveli* Pillai, 1961	Ceylon (Sri Lanka)	Ariake Sea, Maizuru Bay (Korea, Yellow Sea, South China Sea)	"Kani-gokai," 8–60 m deep	Imajima (1972, 1996), Wu et al. (1985), and Paik (1989)
Nereidinae					
Leonnates	*L. persicus* Wesenberg-Lund, 1949	Persian Gulf	Western Japan (Yellow Sea, South China Sea)	"Perusha-gokai," less than 30 m deep, EM-1	Wu et al. (1985) and Sato and Kubo (2009)
	L. nipponicus Imajima, 1972	Koniya, Amami-oshima	only type locality (Korea)	"Hanaguro-gokai," among corals	Imajima (1972, 1996) and Paik (1989)
Tylorrhynchus	*T. osawai* (Izuka, 1903) (= *T. heterochaetus* sensu Imajima, 1972) (= *Ceratocephale osawai* Izuka, 1903)	Japan	Hokkaido to Ryukyu Arc (Russian Far East, Korea)	"Itome," upper intertidal in estuaries, EM-2	Imajima (1972, 1996), Khlebovich (1996), and Sato (unpublished data)

(continued)

Table 19.1 (continued)

Subfamily genus	Name of species (synonym)	Type locality	Distribution in Japan and (neighboring countries)	"Japanese name," habitats, and remarks[a]	References
Cheilonereis	*C. cyclurus* (Harrington, 1897)	Washington, Northeast Pacific	Hokkaido and northern Honshu (Russian Far East, Korea, Yellow Sea)	"Erimaki-gokai," commensal with a hermit crab, *Pagurus ochotensis*	Imajima (1972, 1996), Wu et al. (1985), Paik (1989), and Khlebovich (1996)
Nicon	*N. moniloceras* (Hartman, 1940)	California, Northeast Pacific	Hokkaido to Tsushima (Yellow Sea)	"Gomafu-gokai," 20–200 m deep	Imajima (1972, 1996) and Wu et al. (1985)
	N. japonicus Imajima, 1972	Ariake Sea, Kyushu, Japan	Only type locality (South China Sea)	"Ariake-gokai," 10–50 m deep	Imajima (1972, 1996) and Wu et al. (1985)
	N. sinica Wu & Sun, 1979	Chinese Continental Shelf	Off Daio-zaki, Mie Prefecture (Yellow Sea, South China Sea)	424–425 m deep	Wu and Sun (1979), Wu et al. (1985), and Miura (1990)
Rullierinereis	*R. misakiensis* (Imajima & Hayashi, 1969) (= *Nikon misakiensis*)	Misaki, central Japan	Only type locality	"Tsubo-gokai," among sessile organisms	Imajima and Hayashi (1969) and Imajima (1972, 1996, 2015)
	R. profunda Imajima, 2009	Off Miyako, northern Japan	Only type locality	"Kagitsume-gokai," 2018 m deep	Imajima (2009, 2015)
Ceratonereis	*C. mirabilis* Kinberg, 1866	Brazil	Northern Honshu to Ryukyu Arc (Korea, South China Sea)	"Futamata-gokai," less than 55 m deep, cosmopolitan, EM-1	Imajima (1972,1996, 2003), Wu et al. (1985), and Paik (1989)
	C. japonica Imajima, 1972	Koniya, Amami-oshima	Only type locality (South China Sea)	"Kirekomi-gokai," intertidal sandy bottom, EM-1	Imajima (1972, 1996) and Wu et al. (1985)
Composetia	*C. hircinicola* (Eisig, 1870)	Naples, Italy	Middle Honshu to Ryukyu Arc (Korea, South China Sea)	"Futasuji-gokai," less than 145 m deep, EM-1	Imajima (1972, 1996, 2003), Wu et al. (1985), and Paik (1989)
	(=*Ceratonereis hircinicola*)				
	(=*Ceratonereis* (*Composetia*) *hircinicola*)				

	C. moorei (Imajima, 1972)	Suruga Bay, middle Japan	Kurile Islands to middle Honshu	"Mua-gokai," 110–140 m deep	Moore (1903), Izuka (1912), and Imajima (1972, 1996)
	(=*Nereis pusilla* Moore, 1903)				
	(=*Ceratonereis* (*Composetia*) *moorei*)				
	C. costae (Grube, 1840)	Mediterranean Sea	Sagami Bay (South China Sea)	"Minami-gokai," 45–60 m deep, cosmopolitan, EM-1	Wu et al. (1985) and Imajima (2003, 2015)
	(=*Ceratonereis costae*)				
	C. sp. 1		Ryukyu Arc	Undescribed species, estuaries	Sato et al. (2014)
	C. sp. 2 (=*Ceratonereis (Composetia)* sp. sensu Sato, 2012)		Ryukyu Arc	"Kumejima-nagare-gokai," undescribed species, estuaries	Sato (2012) and Sato et al. (2014)
Simplisetia	*S. erythraeensis* (Fauvel, 1918)	Gulf of Aden	Hokkaido to Ryukyu Arc (Korea, Yellow Sea, South China Sea)	"Koke-gokai," intertidal, with a mucous tube covered with sand	Imajima (1972, 1996), Wu et al. (1985), Paik (1989), and Yamanishi and Sato (2007)
	(=*Ceratonereis erythraeensis*)				
Platynereis	*P. bicanaliculata* (Baird, 1863)	Canadian coast of Northeast Pacific	Hokkaido to Ryukyu Arc (Korea, Yellow Sea, Taiwan, East and South China Sea)	"Tsuruhige-gokai," less than 30 m deep, EM-1	Wu (1967), Imajima (1972, 1996, 2003), Wu et al. (1985), and Paik (1989)
	P. dumerilii (Audouin & M. Edwards, 1833)	La Rochelle, France	Middle Honshu to Ryukyu Arc (Korea, Taiwan, South China Sea)	"Iso-tsuruhige-gokai," cosmopolitan	Wu (1967), Imajima (1972, 1996, 2003), Wu et al. (1985), and Paik (1989)
	P. australis (Schmarda, 1861)	New Zealand	Southern Japan (Western Australia)	"Minami-tsuruhige-gokai," intertidal	Imajima (1972, 1996)
Perinereis	*P. suluana* (Horst, 1924)	Sulu Archipelago Philippines	Oura Bay, Okinawa-jima Island (Indo-West Pacific)	"Shiroeri-gokai," 7–35 m deep, EM-1	Tanaka (2016)

(continued)

Table 19.1 (continued)

Subfamily genus	Name of species (synonym)	Type locality	Distribution in Japan and (neighboring countries)	"Japanese name," habitats, and remarks[a]	References
	P. *cultrifera* (Grube, 1840)	Naples, Italy	Northern Honshu to Ryukyu Arc (Korea, Yellow Sea, Taiwan)	"Kumadori-gokai," less than 20 m deep, cosmopolitan, EM-1	Wu (1967), Imajima (1972, 1996, 2003), Wu et al. (1985), and Paik (1989)
	P. *linea* (Treadwell, 1936)	Amoy (=Xiamen), China	Sumida-gawa River, Tokyo (Korean and Chinese coasts of Yellow Sea)	"Ao-gokai," intertidal, established in the western Mediterranean as an invader population, EM-1	Wu (1967), Imajima (1972, 1996), Wu et al. (1985), Paik (1989), Arias et al. (2013), and Sakaguchi et al. (unpublished data)
	(=*P*. *vancaurica tetradentata* sensu Imajima, 1972)				
	(=*P*. *aibuhitensis* sensu Imajima, 1996)				
	P. *wilsoni* Glasby and Hsieh, 2006	Taipei, Taiwan	Hokkaido to Ryukyu Arc (Korea, Taiwan, Hong Kong)	"Ishi-iso-gokai," intertidal, EM-1	Imajima (1972, 1996, 2003), Glasby and Hsieh (2006), and Park and Kim (2007)
	(=*P*. *nuntia* var. *vallata* sensu Imajima, 1972)				
	(=*P*. *nuntia vallata* sensu Imajima, 1996, 2003)				
	P. *mictodonta* (Marenzeller, 1879)	Japan	Hokkaido to Ryukyu Arc (Korea, China, Taiwan)	"Suna-iso-gokai," intertidal, EM-1	Imajima (1972, 1996), Glasby and Hsieh (2006), and Park and Kim (2007)
	(=*P*. *nuntia* var. *brevicirris* sensu Imajima, 1972)				
	(=*P*. *nuntia brevicirris* sensu Imajima, 1996)				
	P. *neocaledonica* Pruvot, 1930	Noumea, New Caledonia	Ryukyu Arc (Taiwan)	"Futoyubi-gokai," intertidal	Wu (1967), Imajima et al. (1985), and Imajima (1996)

Pseudonereis	*P. gallapagensis* Kinberg, 1866	Galapagos Island	Ryukyu Arc (Korea, Taiwan, South China Sea)	"Yarisaki-gokai," EM-1	Wu (1967), Imajima (1972, 1996), Wu et al. (1985), Paik (1989), and Sato (unpublished data)
	P. variegata (Grube, 1856)	Valparaiso, Chile	Throughout Japan (Korea, Yellow Sea, South China Sea)	"Dengaku-gokai," EM-1	Imajima (1972, 1996), Wu et al. (1985), Paik (1989), and Sato (unpublished data)
	P. anomala Gravier, 1901	Djibouti, Gulf of Aden	Middle Honshu to Ryukyu Arc (Korea, Taiwan, South China Sea)	"Rotto-gokai" = "Usuzumi-gokai," intertidal or shallow subtidal, EM-1	Okuda (1938), Wu (1967), Imajima (1972, 1996, 2003), Wu et al. (1985), Paik (1989), and Bakken (2007)
	(=*P. rottnestiana* Augener, 1913)				
	(=*N. nichollsi* Kott, 1951)				
Hediste	*H. japonica* (Izuka, 1908)	Kojima Bay in Seto Inland Sea, Japan	Western Japan (Yellow Sea)	"Ariake-kawa-gokai," intertidal mudflats in estuaries, EM-3	Sato and Nakashima (2003) and Sato and Sattmann (2009)
	(=*Nereis japonica* Izuka, 1908)				
	(=*Hediste* sp. 2 (Ariake form) sensu Sato, 1999)				
	H. diadoroma Sato and Nakashima, 2003	Kagoshima, southern Kyushu, Japan	Hokkaido to Kyushu (Yellow Sea ?)	"Yamato-kawa-gokai," estuarine intertidal, established in Northeast Pacific coasts of USA as invader populations, EM-3	Sato and Nakashima (2003) and Nishizawa et al. (2014)
	(= Small-egg type of *Neanthes japonica* sensu Sato & Tsuchiya, 1987, 1991, Sato & Ikeda, 1992)				
	(= Small-egg form of *Hediste japonica* sensu Sato & Masuda, 1997, Sato, 1999)				

(continued)

Table 19.1 (continued)

Subfamily genus	Name of species (synonym)	Type locality	Distribution in Japan and (neighboring countries)	"Japanese name," habitats, and remarks[a]	References
	H. atoka Sato & Nakashima, 2003	Aomori, northern Honshu, Japan	Throughout Japan (Korea)	"Hime-yamato-kawa-gokai," estuarine intertidal, NE	Sato and Nakashima (2003) and Tosuji and Sato (2010)
	(= Large-egg type of *Neanthes japonica* sensu Sato & Tsuchiya, 1987, 1991, Sato & Ikeda, 1992)				
	(= Large-egg form of *Hediste japonica* sensu Sato & Masuda, 1997, Sato, 1999)				
Alitta	*A. brandti* Malmgren, 1865	Arctic Ocean	Hokkaido to northern Honshu (Russian Far East, Northeast Pacific, Korea)	"Jamushi," EM-3	Izuka (1912), Imajima (1972, 1996), Paik (1989), and Khlebovich (1996)
	(=*Nereis dyamushi* Izuka, 1912)				
	(=*Neanthes virens* sensu Imajima, 1972,1996)				
Neanthes	*N. pachychaeta* (Fauvel, 1918)	Madagascar	Middle and southern Japan (South China Sea)	"Kebuto-gokai," less than 274 m deep, widespread in the Indo-Pacific, EM-1	Imajima (1972, 1996, 2003), Wu et al. (1985), and Glasby et al. (2011)
	(=*Ceratonereis pachychaeta* Fauvel, 1918)				
	N. cf. *glandicincta* (Southern, 1921)		Southern Kyushu to Ryukyu Arc (Taiwan)	"Samidori-gokai," estuaries, undescribed species similar to *N. glandicincta*, NE	Wu (1967), Uchida (1990), and Sato et al. (2013, unpublished data)
	(=*Ceratonereis burmensis* sensu Uchida, 1990)				

	N. caudata (Delle Chiaje, 1822)	Naples, Italy	Hokkaido to Kyushu (Korea, Philippines, Australia)	"Hime-gokai," cosmopolitan	Imajima (1972, 1996, 2003) and Paik (1989)
	N. unifasciata (Willey, 1905)	Gulf of Mannar, India	Chichi-jima Island, Ogasawara Islands (South China Sea)	"Uirei-gokai," 50–88 m deep, tropical Indo-West Pacific, EM-1	Wu et al. (1985), Bakken and Wilson (2005), and Imajima (2015)
	N. succinea (Leuckart, 1847)	Helgoland, German North Sea	Middle Honshu to northern Kyushu (Russian Far East, Korea, China)	"Ashinaga-gokai," in or around estuaries, less than 50 m deep, nonnative species, EM-1	Imajima (1972, 1996), Paik (1989), and Sato (2013)
	(=*Alitta succinea*)				
Nectoneanthes	*N. oxypoda* (Marenzeller, 1879)	Yokohama, Japan	Northern Honshu to Kyushu (Russian Far East, Korea, China)	"Ougi-gokai," less than 100 m deep, EM-1	Marenzeller (1879), Imajima (1972, 1996), Paik (1989), and Sato (2013)
	(=*N. latipoda* Paik, 1973)				
	(=*N. ijimai* (Izuka, 1912))				
	N. uchiwa Sato, 2013	Kojima Bay in Seto Inland Sea, Japan	Seto Inland Sea, Ariake Sea (Korea, China)	"Uchiwa-gokai," estuarine mudflats, less than 20 m deep, EM-1	Imajima (1972, 1996), Paik (1989), and Sato (2013)
	(=*N. oxypoda* sensu Imajima, 1972,1996)				
Nereis	*N. abyssa* Imajima, 2009	Off Sanriku, Japan	Only type locality	"Shinkai-gokai," 150–1500 m deep	Imajima (2009, 2015)
	N. denhamensis Augener, 1913	Western Australia	Hachijo-jima and Amami-oshima Islands (Korea, South China Sea)	"Ooba-gokai," intertidal, EM-1	Imajima (1972, 1996), Wu et al. (1985), and Paik (1989)
	N. heterocirrata Treadwell, 1931	Japan	Hokkaido to Kyushu (Korea, Yellow Sea, East China Sea, Taiwan)	"Higebuto-gokai," intertidal or among sessile organisms, EM-1	Wu (1967), Imajima (1972, 1996), Wu et al. (1985), and Paik (1989)
	N. izukai Okuda, 1939	Off Kinkazan, northern Japan	Only type locality	"Izuka-gokai," muddy bottom 230 m deep	Okuda (1939) and Imajima (1972, 1996)
	N. multignatha Imajima & Hartman, 1964	Japan	Hokkaido to Ryukyu Arc (Korea, Yellow Sea, East China Sea)	"Masago-gokai," endemic to East Asia, less than 150 m deep, EM-1	Imajima (1972, 1996, 2003), Wu et al. (1985), and Paik (1989)

(continued)

Table 19.1 (continued)

Subfamily genus	Name of species (synonym)	Type locality	Distribution in Japan and (neighboring countries)	"Japanese name," habitats, and remarks[a]	References
	N. neoneanthes Hartman, 1948	Alaska	Hokkaido to Ryukyu Arc (Korea, Yellow Sea, East China Sea)	"Yasuri-gokai," intertidal or among sessile organisms, EM-1	Imajima (1972, 1996, 2003), Wu et al. (1985), and Paik (1989)
	N. pelagica Linnaeus, 1758	Western Europe	Hokkaido to Ryukyu Arc (Russian Far East, Korea, Yellow Sea, East China Sea)	"Futsuu-gokai," less than 120 m deep, widespread in the north temperate zone, EM-1	Imajima (1972, 1996, 2003), Wu et al. (1985), Paik (1989), and Khlebovich (1996)
	N. surugaense Imajima, 1972	Suruga Bay, central Japan	Only type locality (Korea, South China Sea as a subspecies, *N. surugaense nanhaiensis* Sun & Shen, 1978)	"Suruga-gokai," muddy bottom 910–1430 m deep	Imajima (1972, 1996), Wu et al. (1985), and Paik (1989)
	N. vexillosa Grube, 1851 (=*N. ezoensis* Izuka, 1912)	Sea of Okhotsk	Hokkaido to middle Honshu (Russian Far East, Northeast Pacific, Korea, Yellow Sea)	"Ezo-gokai," intertidal or subtidal *Zostera* beds, EM-1	Imajima (1972, 1996), Wu et al. (1985), Paik (1989), and Khlebovich (1996)
	N. zonata Malmgren, 1867 (=*N. cylindrata* Ehlers, 1868)	Arctic Ocean	Hokkaido to Kyushu (Russian Far East, Korea, Yellow Sea)	"Nishiki-gokai," less than 210 m deep, widespread in the north temperate zone	Imajima (1972, 1996, 2003), Wu et al. (1985), Paik (1989), and Khlebovich (1996)

[a] *EM-1* epitoky into the typical heteronereis form, *EM-2* epitoky into a modified heteronereis form, *EM-3* epitoky into non-heteronereid forms, *NE* no epitokous metamorphosis

Many nereidids show swarming behavior (mass-swimming of sexually mature adults) to shed gametes freely into the water, accompanied by a common drastic morphological change (known as epitokous metamorphosis) into epitokes of the 'heteronereis form' in both males and females or in males only, that is, marked enlargement of the eyes, division of the body into two or three parts, enlargement and/or deformation of the parapodial ligules and cirri with addition of some lappets (most marked in the middle or posterior body), and all or most chaetae replaced by paddle-like natatory chaetae (Clark 1961; Schroeder and Hermans 1975) (Figs. 19.1g, 19.2). The modification in the heteronereis form is almost uniform among many species beyond generic differences. The change to the heteronereis form seems to be adaptive, serving to increase swimming ability, which enables the adults to swim at high speed to escape from carnivores for their successful spawning. However, some species spawn without any epitokous metamorphosis and swarming.

The epitokous metamorphosis into the typical heteronereis form has been known in 25 of all 54 Japanese nereidids (shown as EM-1 in Table 19.1).

19.2.4 Chromosomal Sex Determination

Diploid chromosome numbers ranging from 18 to 38 with dominance of 28 are previously reported in 18 species of Nereididae (Christensen 1980; Pesch and Pesch 1980; Pesch et al. 1988; Weinberg et al. 1990, 1992; Sato and Ikeda 1992; Zheng et al. 1992; Lipari et al. 1994; Jha et al. 1995; Tosuji et al. 2004, 2010; Ipucha et al. 2007; Leitão et al. 2010).

The presence of an XX–XY (male heterogametic) sex chromosome system, wherein the Y chromosome is larger than the X chromosome, has been demonstrated in three Japanese dioecious species of *Hediste* (Sato and Ikeda 1992; Tosuji et al. 2004). A similar chromosomal dimorphism implying the presence of sex chromosomes was also reported in a population of *Neanthes* cf. *acuminata* (Pesch and Pesch 1980). Once extreme sex chromosome differences evolve, the evolution of new sex-determining mechanisms may be prevented, and species descended from a common ancestor will share the same sex chromosome system (Bull 1983). Therefore, it seems probable that many nereidid species have the XX–XY system in common. An exceptional hermaphroditic species, *Hediste limnicola*, is known to have a diploid chromosome number of 26 (Tosuji et al. 2010), whereas all other four species of *Hediste* have that of 28 (Sato and Ikeda 1992; Tosuji et al. 2004; Leitão et al. 2010). The evolution of hermaphroditism in *H. limnicola* may be associated with loss of a pair of sex chromosomes from the 28-chromosome set in the ancestral form (Tosuji et al. 2010).

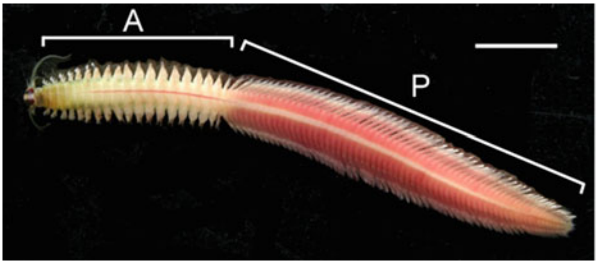

Fig. 19.2 Epitokous male of the typical heteronereis form in *Platynereis bicanaliculata*. The body is divided into the anterior (*A*) and posterior (*P*) parts. Specimen collected from Tateyama (Chiba Prefecture) in Tokyo Bay on 6 April 2008. (Photographed by Masato Kiyomoto.) *Bar* 5 mm

19.3 Estuarine Nereidid Fauna in Japan

Estuaries are characterized by having a constantly changing mixture of saltwater and freshwater, and by being dominated by fine sedimentary material carried from the sea and rivers, which accumulates there to form mudflats (McLusky and Elliott 2004). In Japanese estuaries, about 15 species of Nereididae have been found, showing their species-specific ranges in the distribution along the salinity gradient in estuaries (Fig. 19.3).

19.3.1 Taxonomy of Two Nectoneanthes *and an Alien* Neanthes *Species*

For a long time, there had been a serious taxonomic confusion with respect to two species of *Nectoneanthes*, as well as *Neanthes succinea*. The genus *Nectoneanthes* Imajima, 1972 was reduced to a junior synonym of *Neanthes* Kinberg, 1865 by Wilson (1988), because the type species of *Nectoneanthes* (*N. oxypoda*) was regarded as a junior synonym of *Neanthes succinea*. Thereafter, *Nectoneanthes* was regarded as a junior synonym of the genus *Alitta* Kinberg, 1865, because *Neanthes succinea* was transferred to *Alitta* by Bakken and Wilson (2005). Recently, however, the combination *Neanthes succinea* was resurrected, reversing the placement in *Alitta* by Sato (2013), who showed that an important newly found characteristic of *Neanthes succinea*, the presence of notoaciculae on chaetigers 1 and 2, was not shared by the *Alitta* species. Sato (2013) also resurrected the genus *Nectoneanthes*, with evidence showing that *Nectoneanthes oxypoda* is not a junior synonym of *Neanthes succinea*, but a valid species. The genus *Nectoneanthes* is currently composed of only two species, *N. oxypoda* (Marenzeller, 1879) and *N. uchiwa* Sato, 2013; the other six species previously referred to as *Nectoneanthes*, including *N. ijimai* (Izuka, 1912) and *N. latipoda* Paik, 1973 (previously recorded in Japanese fauna), were judged to be junior synonyms of *N. oxypoda* (Sato 2013).

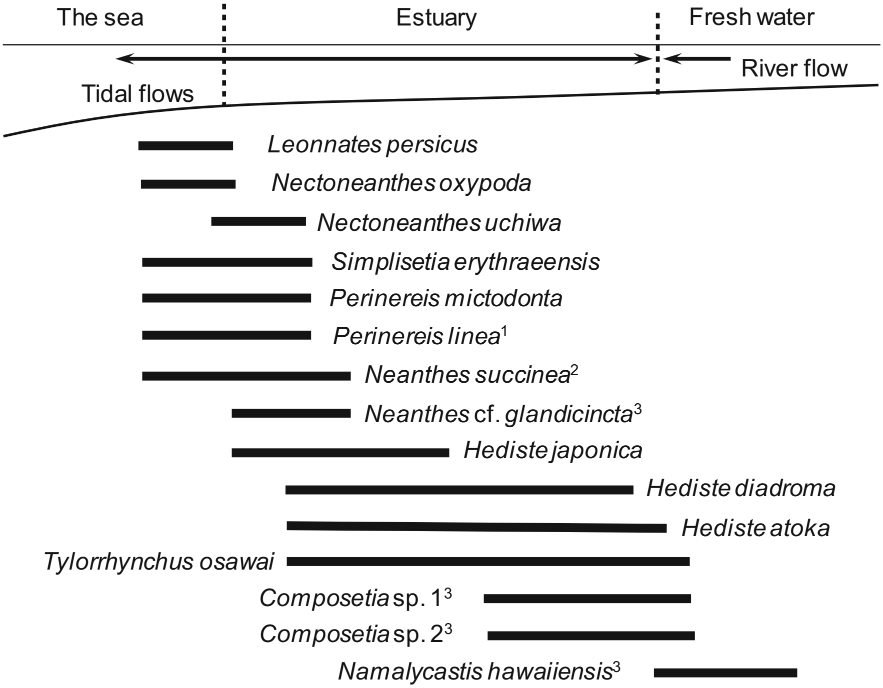

Fig. 19.3 Schematic diagram of longitudinal section of an estuary and adjacent habitats along a river, with approximate distributions of 15 nereidids (adults) in Japanese estuaries. *1* Collected from only Sumida-gawa River in Tokyo Bay (detailed locality unknown) in 1908. The habitat range is estimated based on the Korean habitats of this species. *2* Non-indigenous species. *3* Found only in southern Japan (mostly only in the Ryukyu Islands)

Nectoneanthes uchiwa has been confused with *N. oxypoda* since the early studies made by Japanese taxonomists (Izuka 1912; Okuda 1933; Imajima 1972), who redescribed '*N. oxypoda*' incorrectly using specimens of *N. uchiwa*. The confusion led to *N. oxypoda* being described again as a new species in several regions such as in Korea by Paik (1973, as *N. latipoda*).

Nectoneanthes uchiwa is endemic to eastern Asia, usually inhabiting intertidal muddy bottoms in the lower reaches of estuaries, with the present Japanese distribution limited to western Seto Inland Sea, the Ariake Sea, and the Shiranui (Yatsushiro) Sea, now designated as a 'vulnerable' species by the Japanese Association of Benthology (2012). On the other hand, *N. oxypoda* is widely distributed along the coasts of Asia and Australia, usually inhabiting subtidal sandy or muddy bottoms around the mouth of estuaries.

Neanthes succinea is widely distributed in the Northern and Southern Hemispheres at present. However, this species seems to be native to only some coasts of the North Atlantic Ocean, from which it has been introduced to many places in the world in association with increasing cargo transportation by an increasing trade fleet (Wonham and Carlton 2005). In Japan, this species was first recorded by

Imajima (1972) based on specimens collected from Tokyo Bay in 1964, although this species did not appear in the earlier literature on polychaete fauna (Marenzeller 1879; Izuka 1912; Imajima and Hartman 1964). The present distribution of *N. succinea* in Japan is restricted to several regions at or around large international ports (e.g., Tokyo Bay, Ise Bay, and Osaka Bay in Honshu, and Dokai Bay in northern Kyushu) or to where original estuarine habitats have been severely damaged by anthropogenic coastal developments (e.g., Kojima Bay in Seto Inland Sea, and Lake Nakaumi in Shimane Prefecture) (Sato 2013).

19.3.2 Euryhaline Hediste *and* Tylorrhynchus *Species*

Hediste and *Tylorrhynchus* species are euryhaline with a wide distribution along estuaries. These species often attain high density and biomass in local populations, for example, biomass in wet weight up to 990 g/m^2 (as *H. japonica* alone) in the lower reaches of Omuta-gawa River in the Ariake Sea and 660 g/m^2 (as *T. osawai* alone) in the upper reaches of the same estuary (Hanafiah et al. 2006), having ecologically important functions in nutrient cycling in an estuary ecosystem (Tsuchiya and Kurihara 1979; Sayama and Kurihara 1983; Kikuchi 1986). Their life histories are described next.

19.3.3 Perinereis linea *with a Question: Native or Not?*

A large number of annelid worms have been traded and commercially sold alive as fishing bait worldwide, increasing the risk of accidental introduction of exotic invaders (Arias et al. 2013). *Perinereis linea* (Treadwell, 1936) commonly inhabits mudflats at the upper littoral zone in the Korean and Chinese coasts of the Yellow Sea and the East China Sea, and since the early 1970s has been caught abundantly and exported to Japan and even to Europe as one of the most common baitworms for recreational fishing (Choi and Lee 1997; Saito et al. 2011, 2014). A large number of unused or fragmented baitworms seem to have been discarded into Japanese and European coastal waters by fishermen. As suspected, a nonnative population of *P. linea* has been established in Mar Menor lagoon (Spain) in the western Mediterranean (Arias et al. 2013). In Japan, however, no established population of *P. linea* has been recorded, although this species is treated as a nonnative invader (The Ecological Society of Japan 2002) and some live specimens, which may have been just discarded by anglers, have been found in and around Tokyo Bay (Iwasaki et al. 2004; Nishi and Kato 2004; Nishi 2005; M. Taru, personal communication). In a large survey of macrobenthic organisms in tidal flats in 157 sites covering the whole of Japan from 2002 to 2004, *P. linea* was not found anywhere (Yamanishi and Sato 2007).

However, there is a single precious specimen of *P. linea* that was collected from Sumida-gawa River in Tokyo Bay in 1908 and has been preserved in the National Museum of Nature and Science, Tsukuba, Japan. Imajima (1972) described this specimen as a new subspecies, *P. vancaurica tetradentata*, which was later synonymized with *P. aibuhitensis* (Grube, 1878) by Lee et al. (1992) (see also Imajima 1996). Recently, however, Arias et al. (2013) showed evidence that Chinese and Korean specimens of *P. aibuhitensis* sensu Lee et al. (1992) belong to *P. linea*, showing that *P. linea* [type locality: Amoy (=Xiamen), China] is a valid species distinct from *P. aibuhitensis* (type locality: Philippines), although *P. linea* was reduced to a junior synonym of *P. aibuhitensis* by Hartman (1938) and Lee et al. (1992). Therefore, in the present chapter, *P. vancaurica tetradentata* is regarded as a junior synonym of *P. linea*. This conclusion is supported by our examination of the type specimen of *P. vancaurica tetradentata* (T. Sakaguchi et al., in preparation).

One single specimen of *P. linea* was collected from the Sumida-gawa estuary in Tokyo in 1908, at times when natural mudflats might still have existed there (Sato 2010) and long before the import of foreign baitworms began. This observation suggests that *P. linea* may be a native of Japanese mudflats, but all (or most) of the Japanese populations may have been extirpated by habitat loss resulting from anthropogenic coastal developments in estuarine mudflats. Extreme reduction of the original wide distribution of the Japanese native mudflat fauna by anthropogenic habitat loss in modern history has been well documented in several macrobenthic species, including the estuarine nereidid *Hediste japonica* (Sato and Sattmann 2009; Sato 2010; see following details). These mudflat-specific species have usually survived in the Ariake Sea in western Kyushu, which constitutes the largest area of mudflats remaining in Japan. If *P. linea* was a species native to Japan, it is expected that its original population may be still alive in the Ariake Sea.

19.3.4 Subtropical Species

Four species (*Neanthes* cf. *glandicincta*, two undescribed species of *Composetia*, and *Namalycastis hawaiiensis*) are distributed only in southern Japan; two undescribed species of *Composetia* occur only in small estuaries in the Ryukyu Islands (Sato 2012; Sato et al. 2014), whereas the other two species have been collected from the Ryukyu Islands and southern Kyushu (Uchida 1990; Glasby 1999; Sato et al. 2013; Sato et al., unpublished data).

Namalycastis hawaiiensis is widespread in the tropical western Pacific, inhabiting freshwaters or very slightly brackish waters in various coastal riparian areas such as streams, swamps, and even in phytotelmata (plant container habitats) (Glasby 1999; Glasby et al. 2003). Glasby (1999) recorded this species from Amami-oshima Island in the Ryukyu Islands based on 14 specimens, which were collected in a stream (freshwater neighboring the upper reaches of the estuary, about 0.5 km upstream from the shore) in Koniya in the southern coast of the island on 24 August 1987 by the present author. Thereafter, additional specimens of putatively the same species have been found from several estuaries in southern Kyushu and five islands of the Ryukyu Islands, although the population densities of this species were very low anywhere (Yamanishi and Sato 2007; Sato et al., unpublished data). The life history of this species is unknown. It is an interesting issue whether this species has a planktonic larval stage in relationship to its dispersal ability among islands. Feuerborn (1931) reported that this species (as *Lycastis ranauensis*) collected from southern Sumatra is hermaphrodite, with both eggs and sperm found in the same individual, but our preliminary examination on the coelomic contents of laboratory-reared worms of this species collected from the Ryukyu Islands suggested the sexes separated (dioecious) (Sato et al., unpublished data). Cryptic speciation may have occurred in "*N. hawaiiensis*."

19.4 Life-History Divergence in *Hediste*

19.4.1 Distributions of Hediste *Species*

Hediste species are commonly distributed in shallow brackish waters of estuaries in the north temperate zone, occurring as representative euryhaline species (Sato 1999, 2004). Five species are currently known: *H. diversicolor* (O. F. Müller, 1776) distributed along both the European and the North American coasts of the Atlantic (Smith 1977), *H. limnicola* (Johnson, 1903) along the North American Pacific Coast (Smith 1958), and three species in Asia (Sato and Nakashima 2003). Facultative filter feeding is known in four of the five species as a unique generic habit of *Hediste* (Harley 1950; Riisgård 1991, 1994; Scaps 2002; Toba and Sato 2013).

Asian *Hediste* specimens were originally identified as *Nereis diversicolor* (=*Hediste diversicolor*) by Marenzeller (1879), but were later described as a new species, *Nereis japonica*, by Izuka (1908). Subsequently, this taxon was found to constitute three distinct but morphologically similar species (Sato and Nakashima 2003): *Hediste japonica* (Izuka, 1908), *H. diadroma* Sato and Nakashima, 2003, and *H. atoka* Sato and Nakashima, 2003.

The *Hediste* species are morphologically very similar to one another. In particular, the three Pacific species *H. diadroma, H. atoka*, and *H. limnicola* are morphologically indistinguishable in sexually immature specimens, whereas *Hediste diversicolor* and *H. japonica* are distinguishable from the other species even in immature specimens by their unique chaetal or parapodial morphology (Smith 1958; Sato 2004). Recently, based on the observation of species-specific morphology at the sexually mature stage, Nishizawa et al. (2014) found that *H. diadroma* inhabited northeast Pacific estuaries (Washington and Oregon, USA), which indicates that this Asian species is established as an exotic invader of the North

American Pacific and may have long escaped detection because of its morphological similarity to the native species (*H. limnicola*). By a further study with a simple molecular method using multiplex polymerase chain reaction (PCR) amplification of the mitochondrial 16S rRNA gene for identification of the three Pacific *Hediste* species (Tosuji and Sato 2012), Tosuji and Furota (2016) demonstrated that the nonnative *H. diadroma* has widely spread into the North American Pacific Coast in Washington, Oregon, and California (USA), coexisting with the native *H. limnicola* at various ratios. *H. diadroma* was dominant in many estuaries in Puget Sound (Washington), and in the Columbia River estuary (Washington and Oregon), suggesting that this species initially invaded estuaries in Washington or northern Oregon; the native *H. limnicola* was dominant in California and at subtidal sites in the Columbia River estuary.

In Japan, both *H. diadroma* and *H. atoka* are widely distributed except for the Ryukyu Islands, where only *H. atoka* is found (Sato and Nakashima 2003; Sato 2004; Tosuji and Sato 2010, 2012). They commonly coexist in the same place, forming a species complex, although their ratio is variable among different sites (Kikuchi and Yasuda 2006; Sato et al., unpublished data).

On the other hand, the present distribution of *H. japonica* is limited to mudflats in the inner part of the Ariake Sea in Japan and on the Korean coast of the Yellow Sea (Sato and Nakashima 2003; Sato 2004, 2006, 2010) (Fig. 19.4). Our examinations of the type and non-type old specimens kept in museum historical collections revealed that the extremely restricted distribution of *H. japonica* in Japan is caused by the rapid reduction of available habitats resulting from recent human impact. Sato and Nakashima (2003) examined the syntype series of *H. japonica*, which were collected from mudflats in the inner part of Kojima Bay in the Seto Inland Sea in 1906 and preserved in the University Museum, the University of Tokyo (as Izuka's collection); one of which was designated as the lectotype. However, the population of the type locality seems to have been extirpated because most of the mudflats were lost to land reclamation by 1956 (Sato 2010). Before that, swarming *Hediste* epitokes (sexually mature worms) were collected by local people, so abundant as to be used as fertilizer for farmlands of a rush (Izuka 1921). There is no recent record of this species from anywhere in the Seto Inland Sea. Moreover, Sato and Sattmann (2009) found non-type specimens of *H. japonica*, which were collected from the innermost part of Ise Bay in central Japan around 1876 and thereafter have been safely preserved in the Natural History Museum in Vienna. This finding indicates that the distribution of *H. japonica* formerly extended to Ise Bay in central Japan. However, the population of *H. japonica* has been extirpated from Ise Bay through recent coastal development; the innermost part of Ise Bay with huge mudflats was almost completely reclaimed to land, where the present large city of Nagoya is located (Sato and Sattmann 2009; Sato 2010). Throughout Japan, about half the tidal flats have already disappeared, mostly during the past 100 years, because of artificial land reclamation (Sato 2010). Consequently, the inner part of the Ariake Sea seems to be the last habitat of *H. japonica* remaining in Japan. Even worse, a recent reclamation project in

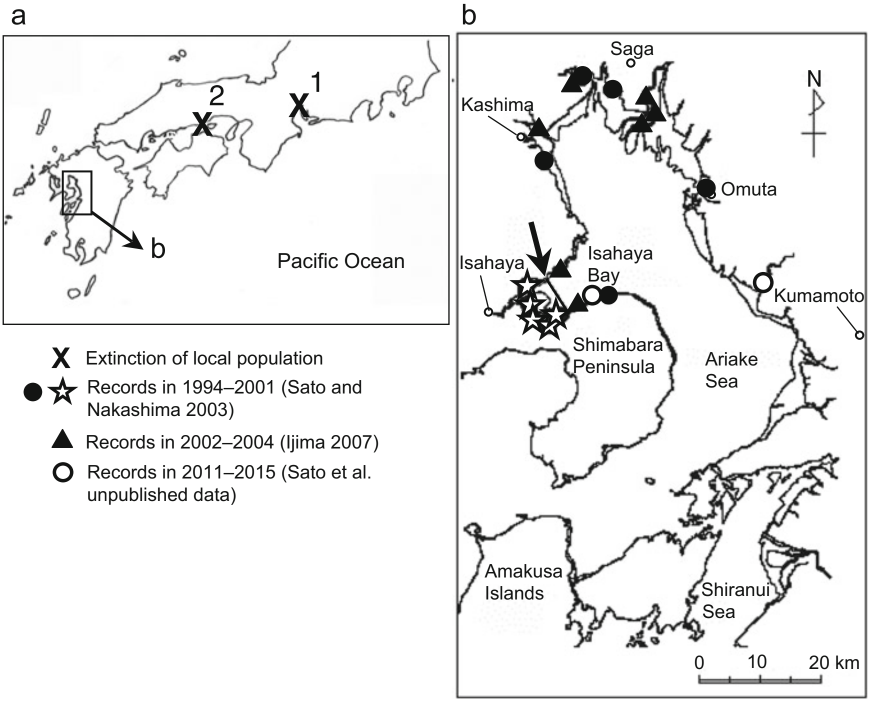

Fig. 19.4 Distribution of *Hediste japonica* in Japan (**a**). The present distribution is limited in the Ariake Sea in Kyushu (**b**). The populations in the inner part of Ise Bay (*1* in **a**) and Kojima Bay in the Seto Inland Sea (type locality) (*2* in **a**) seem to have been extirpated in the twentieth century. Habitats in the inner part of Isahaya Bay in Ariake Sea (*open stars*) were lost after completion of the 7-km-long dike construction for land reclamation in 1997 (*arrow* in **b**)

Isahaya Bay in the inner part of the Ariake Sea caused the loss of a muddy shallow area of about 36 km^2, including the most important habitat for *H. japonica* (Sato and Koh 2004; Sato 2010). This species is now designated as an endangered species in Japan (Japanese Association of Benthology 2012). Reduction of the original wide distribution of estuarine mudflat fauna in Japan into the present narrow one in the inner part of the Ariake Sea has been documented also for some bivalves and a salt marsh plant (Sato 2010).

19.4.2 Differentiation of Life-History Modes

The life-history modes of the five *Hediste* species are remarkably diverse (Table 19.2). Contrasting life cycles are known in the morphologically most similar two species (*H. diadroma* and *H. atoka*) that coexist widely in Japan.

Table 19.2 Comparison of reproductive and developmental characteristics of a *Tylorrhynchus* and five *Hediste* species distributed in the North Temperate Zone

Geographic range and species	Reproductive mode	Remarks on epitoky (change in chaetae)	Egg diameter (μm)	Salinity favorable for development	Remarks on early development	References
Eastern Asia						
Tylorrhynchus osawai	Swarming	Marked modification (replacement by natatory chaetae)	140–160	32	>20-day planktonic larval life	Yamamoto (1947) and Imajima (1972, 1996)
Hediste japonica	Swarming	Slight modification (increase of atokous spinigers)	180–210	22–30	10-day planktonic larval life	Izuka (1908) and Tosuji and Sato (2006)
H. diadroma	Swarming	Slight modification (addition of thin specific spinigers)	130–170	22–30	1-month planktonic larval life	Kagawa (1955), Sato and Tsuchiya (1987, 1991), Sato and Nakashima (2003), and Tosuji and Sato (2006)
H. atoka	Spawning in or around burrows	No epitokous metamorphosis	200–250	9–21	No planktonic larval life, hatching out at 3-chaetiger juvenile	Sato and Tsuchiya (1987, 1991), Kikuchi (1998), Sato and Nakashima (2003), and Sato (2004)
North Atlantic						
H. diversicolor	Female spawns, broods embryos in burrow	No epitokous metamorphosis	195–275	5–27	Demersal larval life in maternal burrows	Dales (1950), Smith (1964), Bartels-Hardege and Zeeck (1990), and Scaps (2002)
Northeast Pacific						
H. limnicola	Hermaphrodite, self-fertilization	No epitokous metamorphosis	120–170	15–20	Viviparity, emerging from parent coelom at 15- to 30-chaetiger juvenile	Smith (1950) and Khlebovich (1996)

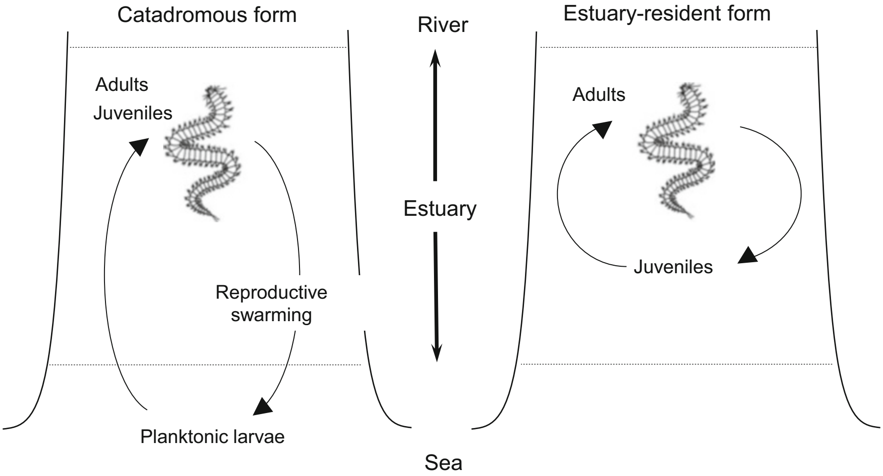

Fig. 19.5 Schematic diagram of two forms of life cycle of euryhaline nereidids in estuaries. Life cycle of catadromous form (*left*) comprises migrations between brackish waters and the sea, characterized by benthic life of juveniles and adults, reproductive swarming of mature adults toward the sea, planktonic life of larvae, and moving upstream and settlement of larvae into brackish waters. Life cycle of estuary-resident form (*right*) completed within brackish waters in estuaries, characterized by reproduction and early development within estuaries. (Modified from Sato 1999)

19.4.2.1 Life Cycle of *Hediste diadroma*

The life cycle of *H. diadroma* is characterized by migration between the adult habitats with low salinity and the larval habitats with high salinity. This type of life cycle is here referred to as the ‘catadromous form’ (Fig. 19.5).

Reproductive swarming of mature adults usually occurs in January to April throughout Japan, with some exceptional records in November in Nakatsu, western Seto Inland Sea, December in the Ariake Sea, and June in Usujiri, Hokkaido (Sato and Tsuchiya 1987; Sato and Nakashima 2003; Hanafiah et al. 2006; Kikuchi and Yasuda 2006; Sato et al., unpublished data) (Fig. 19.6). During swarming, mature adults swim up usually around an hour after night high tide time (or around 2–3 h after evening high tide, adjusting the swarming to be given rise after sunset) during spring tides, and are transported downstream by water currents of the ebb tide, shedding eggs or sperm into the ambient water around the river mouth, where fertilization occurs. After spawning, adults die, having a 1-year lifespan.

The eggs are relatively small (130–170 μm in diameter) and develop into free-swimming trochophore larvae under relatively high salinity (favorable salinity, 22–30) (Tosuji and Sato 2006). After a long planktonic larval life lasting a month or more, the nectochaeta larvae of around six-chaetiger stage move upstream on rising tides, and settle in the upper reaches of estuaries, the adult habitats, with low salinity (Kagawa 1955; Sato et al., unpublished data).

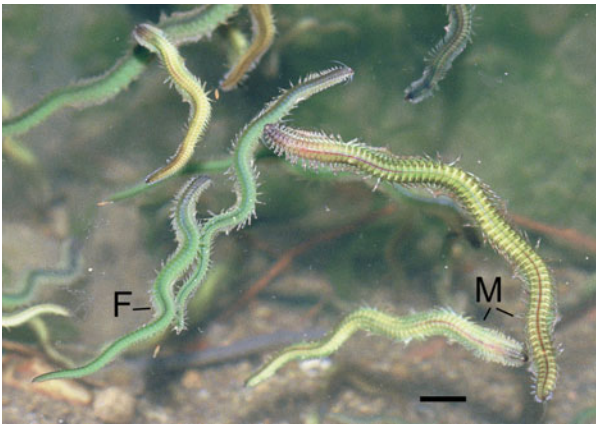

Fig. 19.6 Reproductive swarming of mature females (*F*) and males (*M*) of *Hediste diadroma* at the mouth of the Omoi-gawa River, Kagoshima Prefecture, on 25 February 1986. *Bar* 1 cm. (After Sato and Tsuchiya 1987)

19.4.2.2 Life Cycle of *Hediste atoka*

In contrast, the life cycle of *H. atoka* is completed within low-salinity regions without adult migration toward the sea. This type of life cycle is here referred to as the 'estuary-resident form' (Fig. 19.5).

Many mature adults were collected from sediment samples in late September to October, but a few were found throughout almost the whole year in Kagoshima Prefecture, southern Japan (Sato and Tsuchiya 1987; Sato 1999, 2004). In Miyagi Prefecture, northern Japan, Kikuchi (1998) and Kikuchi and Yasuda (2006) showed that reproduction occurred in a long period from February to October, and that two generations exist per year, with spring recruits reproducing during the following autumn and the autumn recruits reproducing during the following spring.

In our laboratory observation on the mature adults collected in Kagoshima, females spawned within the burrows in aquaria, and males seemed to release sperm near the opening of the female burrows (Sato 2004). Therefore, the sperm may be incorporated into a female burrow by a water current made by the wriggling behavior of a female. However, Kikuchi (1998) observed that mature males and females crawled out of the sediment and released gametes while they crept on the sediment surface in aquaria, and he also collected mature males and females that were swimming in field waters (Miyagi Prefecture, northern Japan). The difference in spawning behavior between populations of southern and northern Japan may be associated with the genetic differentiation among the populations of *H. atoka* (see following). Within sediments, we could find spent adults that were alive for a while after spawning (Sato and Tsuchiya 1987). It is unknown whether the spent adults brood the young. In *H. diversicolor* in the German North Sea, Bartels-Hardege and Zeeck (1990) suggested that the fertilized eggs remaining inside the maternal burrow are protected by the female.

The eggs are relatively large (200–250 μm in diameter). The embryo develops under relatively low salinity (favorable salinity, 9–21; Sato and Tsuchiya 1987). The embryos develop while remaining confined within a relatively solid jelly layer and pass a trochophore stage. Thus, development of *H. atoka* is, in fact, indirect by anatomic standards but direct in functional terms, without a true planktonic phase (Sato and Tsuchiya 1991; Sato 1999). The three-chaetiger nectochaetae hatch out of the jelly layer and soon begin a benthic life, although advanced juveniles with four or more chaetigers can temporarily swim during flood tides. Kikuchi (1998) and Kikuchi and Yasuda (2006) also showed that juveniles with four or five chaetigers could disperse most actively within an estuary by their swimming behavior. Thus, it seems that the juveniles are mainly benthic, and only during flood tides do they float up and swim into the water. By this behavior, a dense mass of the young produced by direct development within a female burrow can disperse widely in an estuary without becoming displaced downstream.

19.4.2.3 Life Cycle of *Hediste japonica*

The life cycle of *H. japonica* can be regarded as the 'semi-catadromous form' or an intermediate form between the catadromous and estuary-resident forms.

Reproductive swarming, which is similar to that of *H. diadroma,* was recorded just after high tide at night during spring tides in December to February in the Ariake Sea (Sato and Nakashima 2003; Hanafiah et al. 2006) and former Kojima Bay in the Seto Inland Sea (Izuka 1908). Mature adults swam above the mudflats, which are habitats of the adults in the lower and middle reaches of estuaries, and shed gametes there (Sato and Nakashima 2003).

Eggs of a relatively large size (180–210 μm in diameter) develop into free-swimming trochophore larvae under relatively high salinity (favorable salinity, 22–30, as in *H. diadroma*) (Tosuji and Sato 2006). After a lecithotrophic pelagic life lasting about 10 days, the four-chaetiger (or somewhat older) nectochaetes, in which the lipid droplets of maternal nutrients disappeared and feeding behavior was first observed, seem to settle in the mudflats where the adults live (Izuka 1908; Tosuji and Sato 2006).

19.4.3 Worldwide Comparison of Hediste *Life Histories*

Both of the other two *Hediste* species distributed in the North Atlantic (*H. diversicolor*) and in the Northeast Pacific (*H. limnicola*) share life-cycle characteristics of the estuary-resident form with *H. atoka*, which lacks both epitokous swarming in reproduction and a true planktonic phase in early development, although *H. diversicolor* and *H. limnicola* have some unique characteristics as follows (Table 19.2). In *H. diversicolor*, a demersal development with hatching out at the trochophore stage and aberrant sex ratios with few males were reported (Dales 1950; Smith 1964). *Hediste limnicola*, which inhabits not only estuaries but also freshwater, is very specialized in reproductive characteristics such as hermaphroditism, self-fertilization, and viviparity (Smith 1950).

It is noteworthy that the life cycles of the catadromous and semi-catadromous forms in *Hediste* are only found in eastern Asia (i.e., Japan and its neighboring countries), whereas the life cycle of the estuary-resident form is widespread in the north temperate zone. Moreover, another genus, *Tylorrhynchus*, having a life cycle of the typical catadromous form, is endemic to Asia (see following details). The geographic characteristics of the Asian estuaries may benefit the evolution and maintenance of the catadromous life cycle. Because of the dominance of steep sloping rivers in the mountainous coasts, the Asian coasts seem to be rich in small-sized estuaries (e.g., most Japanese estuaries are less than 30 km long), where the distance between freshwater and marine habitats is short enough for adult and larval migrations in the catadromous life cycle.

19.4.4 Genetic Differentiation Related to Different Life Cycles

The difference in life-cycle characteristics between species of the catadromous and estuary-resident forms seems to result in the differences in degree of dispersal ability and consequent interpopulational genetic differentiation. In species with the life cycle of catadromous form such as *H. diadroma*, where reproduction and early development occur around the mouth of a river under high salinity, the planktonic larvae seem to migrate easily from river to river through the sea, resulting in frequent gene flow among populations. In contrast, in species with the life cycle of estuary-resident form such as *H. atoka*, where reproduction and early development occur within estuaries under low salinity, without a true planktonic phase, the dispersal ability beyond the sea seems to be limited, resulting in limited gene flow among populations. Therefore, the higher interpopulational genetic differentiation is expected in species with the life cycle of the estuary-resident form. In fact, this suggestion was found to be real in the *Hediste* examples by electrophoretic studies of allozymes (Sato and Masuda 1997). Marked differentiation was detected among five populations of *H. atoka* in Japan, whereas the genetic structure of *H. diadroma* was rather homogeneous even between populations from northern and southern Japan. Moreover, the recent analyses of the mitochondrial COI gene suggest that cryptic speciation without morphological differentiation may have occurred between populations of *H. atoka* in southern Japan (Tosuji and Sato 2010). A similar degree of genetic differentiation is also known among European populations of *H. diversicolor*, in which the life cycle resembles that of the estuary-resident form in the Japanese *H. atoka* (Hateley et al. 1992; Fong and Garthwaite 1994; Abbiati and Maltagliati 1996; Scaps et al. 2001; Breton et al. 2003; Virgilio et al. 2009).

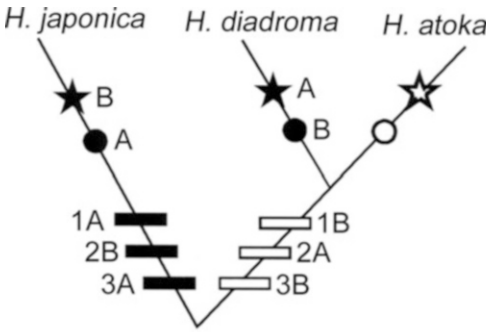

Fig. 19.7 Hypothesis of the phylogenetic relationships in three Asian *Hediste* species. *Stars* indicate reproductive characteristics: *closed stars* reproductive swarming of epitokous adults with (*A*) or without (*B*) addition of epitoke-specific spinigers; *open star* reproduction without swarming and any epitokous metamorphosis. Circular symbols indicate developmental characteristics: *closed circles* pelagic development with a short larval life from middle-sized eggs (180–210 μm in diameter) (*A*), or with a long larval life from small eggs (130–170 μm) (*B*); *open circle* direct development from large eggs (200–250 μm). *Black* and *white rectangles* indicate the contrasting character combinations in immature specimens. *1* Neuropodial homogomph falcigers present (*A*) or absent (*B*). *2* Neuropodial heterogomph spinigers present (*A*) or absent (*B*). *3* Neuropodial postchaetal ligule tapering to digitate lobe throughout (*A*) or only in anterior setigers (*B*). (After Sato and Nakashima 2003)

19.4.5 Evolution of Epitoky

Among the three Asian *Hediste* species, *H. diadroma* and *H. atoka* seem to be most closely related to each other because of their morphological similarity (Fig. 19.7). However, they have contrasting life-history modes, whereas those of *H. diadroma* and *H. japonica* are similar (Table 19.2). Both *H. diadroma* and *H. japonica* show epitokous metamorphosis in combination with their reproductive behavior of swarming, whereas no epitokous metamorphosis occurs in *H. atoka*, corresponding to its reproduction without swarming.

The epitokous metamorphoses in the two *Hediste* species are markedly different from those into the typical heteronereis form prevailing in many marine nereidids in the following characteristics: (1) the segmented trunk is not subdivided into two or three regions each with its specific bristles, parapodia, muscle, etc.; (2) the eyes and parapodial ligules are only slightly enlarged, and no additional lappets are formed in parapodia; (3) the number of spinigers increases in the epitokes, although in two different ways: the number of ordinary homogomph spinigers increases in *Hediste japonica* (Fig. 19.1a), whereas sesquigomph spinigers (Fig. 19.1e), an epitoky-specific type of chaetae, are added in *H. diadroma*; and (4) the absence of natatory chaetae, which are commonly formed in the standard heteronereis epitoky as impressive fan-like sets of paddles. In this context, epitoky in *H. diadroma* and *H. japonica* appear rather inconspicuous and their epitokes swim slowly during swarming in contrast to the epitokes of the standard heteronereis form, which are drastically deformed and swim amazingly fast. In conclusion, the unique epitokous metamorphosis in the two Asian *Hediste* species seems to have evolved independently of those in many other marine nereidids. Moreover, their epitoky seems to have evolved twice independently of each other (Fig. 19.7). The epitoky of a boreal marine species, *Alitta brandti*, which was reported by Imajima (1972, 1996, as *Neanthes virens*), is very similar to that of *H. diadroma*, with the common unique characteristic of the addition of epitoke-specific sesquigomph spinigers (Fig. 19.1e). It would be interesting to know whether this similarity is based on their phylogenetically close relationship.

In *H. diadroma*, we found pre-mature swimming adults from several estuaries in Japan in December to March (Hanafiah et al. 2006; Sato et al., unpublished data). They contained immature oocytes or clusters of spermatogonia or spermatocytes in their coelom. Izuka (1908: p. 297) also reported the probable pre-mature swimming adults of this species (as *Nereis japonica*) in Sumida-gawa River, Tokyo, as follows: "In that river the worm seems to swarm generally once a year in an immature state of development." These findings suggest that at least a part of the pre-mature adults swim to the surface and are transported downstream by the ebb before true swarming. A preliminary move toward the sea by the pre-mature adults seems to be significant in ensuring that they reach the high-salinity regions to perform successful fertilization and early development there. To ensure successful spawning, adults of *H. diadroma* living in the upper reaches of estuaries need to migrate a longer distance downward than those of *H. japonica* that live to the middle reaches of estuaries. The pre-mature swimming behavior has never been recorded in *H. japonica*. In North Atlantic estuaries, the pre-mature swimming behavior similar to that of *H. diadroma* is known in *Alitta virens* (Dean 1978, as *Neanthes virens*).

19.5 Another Unique Epitoky in *Tylorrhynchus*

The genus *Tylorrhynchus* is endemic to Asian estuaries, consisting of only two species: *T. heterochaetus* (Quatrefages, 1865) distributed in tropical and subtropical estuaries in Java, Indonesia (type locality), Vietnam, and southern China (Wu et al. 1985; Khlebovich 1996); and *T. osawai* (Izuka, 1903) in temperate eastern Asia including Japan (type locality), Russian Far East, and Korea (Imajima 1972, 1996; Khlebovich 1996). *Tylorrhynchus osawai* had been regarded as a synonym of *T. heterochaetus* (Imajima 1972, 1996), but was resurrected by Khlebovich (1996), based on obvious morphological differences.

Adults of *T. osawai* commonly inhabit mudflats around reed marshes in the upper littoral zone in estuaries (usually abundant in the upper reaches of estuaries, sometimes penetrating to freshwater). This species has a life cycle of the typical catadromous form (Fig. 19.5), which resembles that of *Hediste diadroma*, including migrations between brackish (or fresh) water and the sea, with relatively small egg size (140–160 μm in diameter) and a long pelagic larval life (more than 20 days) in high-salinity marine regions (Table 19.2). Probably, *T. heterochaetus* has a similar life cycle (Wu et al. 1985).

Reproductive swarming of *T. osawai* has been recorded just after times of high tide during a few nights closely following the new and full moons from September to March (most conspicuous from October to December) (see Hanafiah et al. 2006) (Fig. 19.8f). Before the swarming, adult worms of this species show the epitokous metamorphosis with a unique body-shortening process (Fig. 19.8a–e). At sexual maturity, the anterior portions of the worms, representing about a third of the total body segments of atokes (as many as 300), become filled with eggs or sperm and are transformed into epitokes, which have been colloquially called 'bachi' in Japan (Izuka 1903; Imajima 1972, 1996) (Fig. 19.8c–e). The posterior two thirds of the body degenerates (Fig. 19.8b), shrinks, and usually detaches from the anterior epitokous portion before the epitokes enter reproductive swarming. No other polychaete species forms epitokes this way, except the congeneric *T. heterochaetus* (Pettibone 1971; Wu et al. 1985).

Nevertheless, the mature epitokes of the *Tylorrhynchus* share basic characteristics with the standard heteronereis form (Imajima 1972, 1996), common to the epitokes of many marine nereidids, in the following terms: (1) the residual trunk is subdivided into two parts (Fig. 19.8e); (2) the eyes are enlarged; and (3) atokous chaetae are replaced by paddle-like natatory chaetae in the posterior part of the trunk (Fig. 19.1f). However, the epitokous parapodia of *T. osawai* lack any additional lappets, thus differing from the typical heteronereid form. Thus, the epitokes of *T. osawai* should be regarded as a modified heteronereid form.

During reproductive swarming, the epitokes of *T. osawai* need to migrate a long distance downstream to ensure successful early development. They are transported toward the sea on ebbing tides in spring tides like those of *Hediste diadroma*; salinity approaching full-strength seawater is essential for successful early development (optimum salinity 32; Yamamoto 1947). The following reports indicate that *T. osawai* has a unique adaptation for long-distance migration during reproduction; in laboratory aquaria, swimming epitokes of *T. osawai* shed gametes in media over a wide range of salinity (10–32), where high sperm activity was maintained consistently over 24 h (Miyoshi 1939). Sato and Osanai (1983) demonstrated that *Tylorrhynchus* eggs were fertilizable in media over a wide range of salinity, even down to 20–30 % diluted seawater (salinity, 6–10). These facts indicate that *Tylorrhynchus* epitokes in the field may shed eggs and sperm on the way to the sea even within low-salinity waters, where successful fertilization occurs, and from where the fertilized eggs are transported downwards on ebbing tides, reaching the high-salinity waters for successful development.

The unique epitokous metamorphosis, in which only the anterior one thirds of the body becomes the swimming epitokes, may have also an adaptive significance for secure transportation of the epitokes; the short bodies of epitokes seem to underlie less risk to become tuck with some barriers during the downward drift.

Until around 1900, *T. osawai* was so abundant even in Tokyo that both atokous and epitokous worms of this species were extensively used as fishing bait by fishermen (Izuka 1903). In the brackish-water Lake Hinuma in Ibaraki Prefecture,

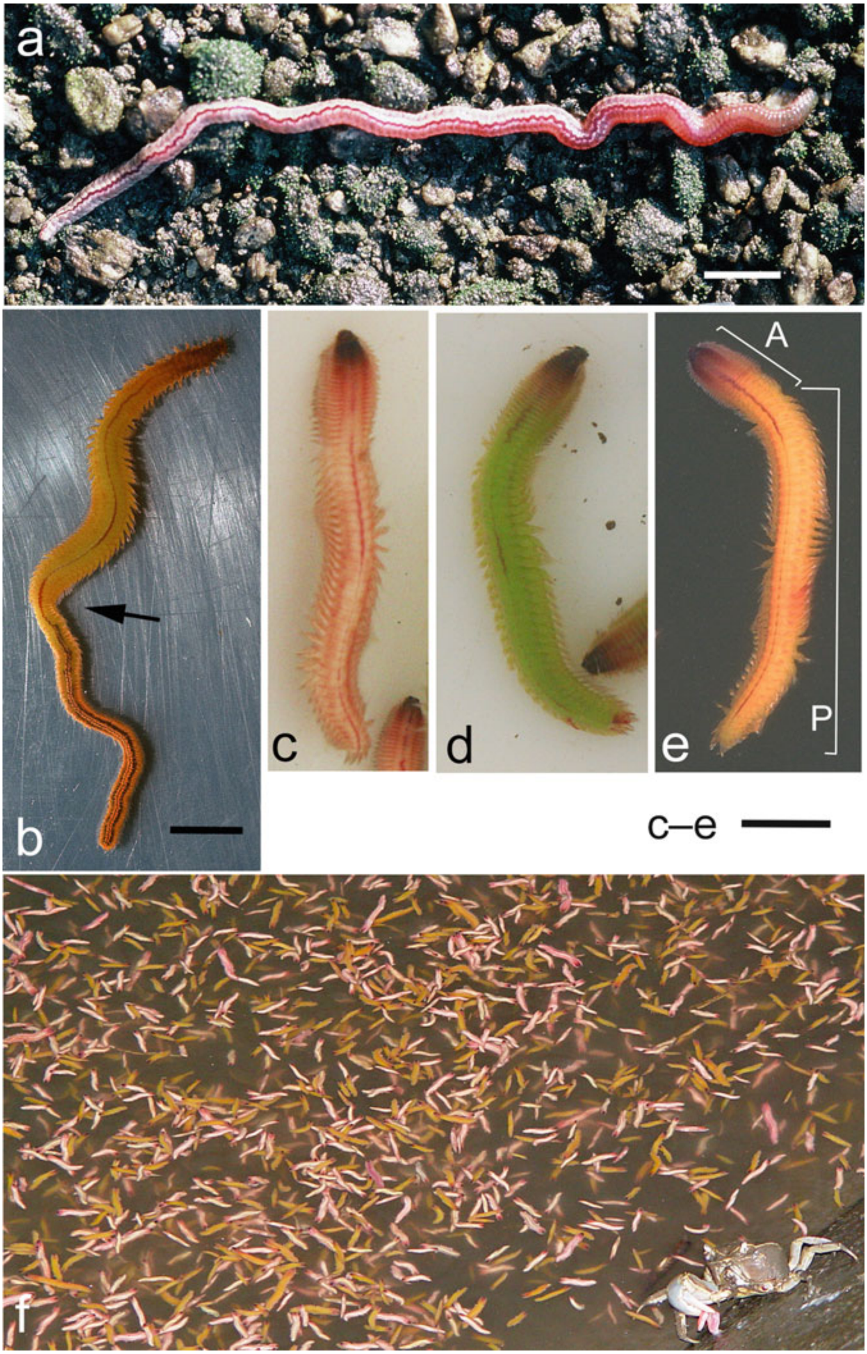

Fig. 19.8 Epitokous metamorphosis and reproductive swarming of *Tylorrhynchus osawai*. **a** Immature atokous worm collected from the Omoi-gawa River, Kagoshima Prefecture. **b** Maturing female in the middle of epitokous metamorphosis. *Arrow* indicates border between the anterior epitokous and the posterior degenerating portions. A specimen collected from

central Japan, numbers of swarming epitokes were formerly collected by local people to use as fertilizer for agricultural fields (Kikuchi 1959). In these ages, this species was known as a pest damaging paddy farming (Inomata 1928). However, the habitats of this species in Japanese estuaries have been severely lost or damaged by recent human impact, as just mentioned. Thus, *T. osawai* is now designated as a "near-threatened" species by Japanese Association of Benthology (2012).

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References

Abbiati M, Maltagliati F (1996) Allozyme evidence of genetic differentiation between populations of *Hediste diversicolor* (Polychaeta: Nereididae) from the western Mediterranean. J Mar Biol Assoc UK 76:637–647

Arias A, Richter A, Anadón N, Glasby CJ (2013) Revealing polychaetes invasion patterns: identification, reproduction and potential risks of the Korean ragworm, *Perinereis linea* (Treadwell), in the Western Mediterranean. Estuar Coast Shelf Sci 131:117–128

Bakken T (2007) Revision of *Pseudonereis* (Polychaeta, Nereididae). Zool J Linn Soc 150:145–176

Bakken T, Wilson RS (2005) Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. Zool Scr 34:507–547

Barnes RSK, Calow P, Olive PJW et al (2001) The invertebrates: a synthesis. Blackwell Science, Oxford

Bartels-Hardege HD, Zeeck E (1990) Reproductive behavior of *Nereis diversicolor* (Annelida: Polychaeta). Mar Biol 106:409–412

Beesley PL, Ross GJB, Glasby CJ (eds) (2000) Polychaetes & allies: the southern synthesis. CSIRO, Melbourne

Breton S, Dufresne F, Desrosiers G, Blier PU (2003) Population structure of two northern hemisphere polychaetes, *Neanthes virens* and *Hediste diversicolor* (Nereididae), with different life-history traits. Mar Biol 142:707–715

Bull JJ (1983) Evolution of sex determining mechanisms. Benjamin/Cummings, London

Choi J-W, Lee J-H (1997) Secondary production of a nereid species, *Perinereis aibuhitensis*, in the intertidal mudflat of the west coast of Korea. Bull Mar Sci 60:517–528

Christensen B (1980) Animal cytogenetics, vol. 2: Annelida. Gebrüder Borntraeger, Berlin

Clark RB (1961) The origin and formation of the heteronereis. Biol Rev 36:199–236

Fig. 19.8 (continued) Asadokoro, Aomori Prefecture on 28 September 1978. **c–e** Swimming epitokous male (**c**) and females (**d**, **e**), collected from the Omuta-gawa River, Fukuoka Prefecture on 16 November 2004. Their bodies are divided into anterior (*A*) and posterior (*P*) parts. Their different body colors are derived from the different colors of coelomic contents seen through their thin transparent body wall, i.e., whitish sperm in the male and green or yellow eggs in the females. (Photographed by Hidetoshi Nakashima.) **f** Swarming of epitokes in the Midori-kawa River, Kumamoto Prefecture on 28 October 2003. A crab (*Helice tridens*) preyed on the swimming epitokes. (Photographed by Mikihide Ezaki.) *Bars* 1 cm

Dales RP (1950) The reproduction and larval development of *Nereis diversicolor* O. F. Müller. J Mar Biol Assoc UK 29:321–360

Dales RP (1963) Annelids. Hutchinson University Library, London

Dean D (1978) Migration of the sandworm *Nereis virens* during winter nights. Mar Biol 45:165–173

Feuerborn HJ (1931) Ein Rhizocephale und zwei Polychaeten aus dem Süßwasser von Java und Sumatra. Verh Internat Verein Theor Angew Limnol 5:618–660

Fong PP, Garthwaite RL (1994) Allozyme electrophoretic analysis of the *Hediste limnicola–H. diversicolor–H. japonica* species complex (Polychaeta: Nereididae). Mar Biol 118:463–470

Fujikura K, Lindsay D, Kitazato H, Nishida S, Shirayama Y (2010) Marine biodiversity in Japanese waters. PloS ONE 5:1–13

Glasby CJ (1999) The Namanereidinae (Polychaeta: Nereididae). Part 1: taxonomy and phylogeny. Rec Aust Mus Suppl 25:1–129

Glasby CJ, Hsieh H-L (2006) New Species and new records of the *Perinereis nuntia* species group (Nereididae: Polychaeta) from Taiwan and other Indo-West Pacific shores. Zool Stud 45:553–577

Glasby CJ, Mogi M, Takahashi K (2003) Occurrence of the polychaete *Namalycastis hawaiiensis* Johnson, 1903 (Nereididae: Namanereidinae) in *Pandanus* leaf axils on Palau, West Pacific. The Beagle 19:97–99

Glasby CJ, Timm T, Muir AI, Gil J (2009) Catalogue of non-marine Polychaeta (Annelida) of the world. Zootaxa 20170:1–52

Glasby CJ, Wilson RS, Bakken T (2011) Redescription of the Indo-Pacific polychaete *Neanthes pachychaeta* (Fauvel, 1918) n. comb. (Annelida, Phyllodocida, Nereididae) and its synonyms. Zoosystema 33:361–375

Hanafiah Z, Sato M, Nakashima H, Tosuji H (2006) Reproductive swarming of sympatric nereidid polychaetes in an estuary of the Omuta-gawa River in Kyushu, Japan, with special reference to simultaneous swarming of two *Hediste* species. Zool Sci 23:205–217

Harley MB (1950) Occurrence of a filter-feeding mechanism in the polychaete *Nereis diversicolor*. Nature (Lond) 165:734–735

Hartman O (1938) Nomenclatural changes involving types of polychaetous annelids of the family Nereidae in the United States National Museum. J Wash Acad Sci 28:13–15

Hateley JG, Grant A, Taylor SM et al (1992) Morphological and other evidence on the degree of genetic differentiation between populations of *Nereis diversicolor*. J Mar Biol Assoc UK 72:365–381

Imabayashi H, Saito H, Ohmasa C et al (1996) Foraging behavior of the polychaete *Halla okudai* in aquariums. Benthos Res Jpn 50:11–17 (in Japanese with English summary)

Imajima M (1972) Review of the annelid worms of the family Nereidae of Japan, with descriptions of five new species or subspecies. Bull Natl Sci Mus Tokyo 15:37–153

Imajima M (1996) Annelida Polychaeta. Biological Research, Tokyo (in Japanese)

Imajima M (2003) Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo (II): orders included within the Phyllodocida, Amphinomida, Spintherida and Enicida. Natl Sci Mus Monogr 23:1–221

Imajima M (2005) About my career in the taxonomic study of Japanese polychaetes. TAXA (Proc Jap Soc Syst Zool) 19:1–7 (in Japanese with English summary)

Imajima M (2009) Deep-sea benthic polychaetes off Pacific coast of the northern Honshu, Japan. Natl Mus Nat Sci Monogr 39:39–192

Imajima M (2015) Annelida Polychaeta IV. Biological Research, Tokyo (in Japanese)

Imajima M, Hartman O (1964) Polychaetous annelids of Japan. Part II. Allan Hancock Found Publ Occas Paper 26:239–452

Imajima M, Hayashi K (1969) Seasonal changes of polychaetes living among the attaching organisms. Proc Jap Soc Syst Zool 5:2–15 (in Japanese with English summary and description)

Imajima M, Tsuchiya M, Nishihira M (1985) Occurrence of *Perinereis neocaledonica* Pruvot, 1930 (Polychaeta: Nereidae) in Southern Japan and some ecological notes on its predator. In: Gillmor RB et al (eds) Special publication of the Mukaishima Marine Biological Station, 1985. Hiroshima University, Onomichi, pp 145–149

Inomata S (1928) Habits and a method of control of *Ceratocephale osawai*, an annelid, which injures the rice plant by cutting its roots. Rep Assoc Jpn Agric Sci Soc 307:246–261 (in Japanese with English summary)

Ipucha MC, Santos CG, Lana PC et al (2007) Cytogenetic characterization of seven south American species of Nereididae (Annelida: Polychaeta): implications for the karyotypic evolution. J Basic Appl Genet 18:15–22

Iwamatsu S, Suzuki A, Sato M (2007) Nereidid polychaetes as major diets for migratory shorebirds at estuarine tidal flats of Fujimae-higata in Japan. Zool Sci 24:676–685

Iwasaki K, Kimura T, Kinoshita K et al (2004) Human-mediated introduction and dispersal of marine organisms in Japan: results of a questionnaire survey by the Committee for the Preservation of the Natural Environment, the Japanese Association of Benthology. Jpn J Benthol 59:22–44 (in Japanese with English summary)

Izuka A (1903) Observation on the Japanese Palolo, *Ceratocephara osawai*, n. sp. J Coll Sci Imp Univ Tokyo 17:1–37, 2 pls

Izuka A (1908) On the breeding habit and development of *Nereis japonica* n. sp. Annot Zool Jpn 6:295–305

Izuka A (1912) The errantiate Polychaeta of Japan. J Coll Sci Imp Univ Tokyo 30:1–262, 24 pls

Izuka A (1921) Animals of favorites. Nisshindo, Tokyo (in Japanese)

Japanese Association of Benthology (2012) Threatened animals of Japanese tidal flats: Red Data Book of seashore benthos. Tokai University Press, Hadano (in Japanese)

Jha AN, Hutchinson TH, Mackay JM, Elliott BM, Pascoe PL, Dixon DR (1995) The chromosomes of *Platynereis dumerilii* (Polychaeta: Nereidae). J Mar Biol Assoc UK 75:551–562

Kagawa Y (1955) Note on the optimum salinities, studied in the adult and larva of the brackish-water polychaete worm, *Nereis japonica*. J Gakugei Coll Tokushima Univ Nat Sci 6:11–16 (in Japanese with English summary)

Kan K, Sato M, Nagasawa K (2016) Tidal-flat macrobenthos as diets of the Japanese eel *Anguilla japonica* in western Japan, with a note on the occurrence of a parasitic nematode *Heliconema anguillae* in eel stomachs. Zool Sci 33:50–62

Khlebovich VV (1996) Fauna of Russia and neighbouring countries. Polychaetous annelids. Volume III. Polychaetes of the family Nereididae of the Russian Seas and the adjacent waters. Russian Academy of Sciences, Zoological Institute, St. Petersburg, n.s. no. 140. Nauka Publishing House (in Russian with English summary)

Kikuchi H (1959) Ecological study on the so-called Japanese Palolo, *Tylorrhynchus heterochaetus* Quatrefages. 1. Swarming in Lake Hinuma, Ibaraki Prefecture. Bull Fac Lib Arts Ibaraki Univ Nat Sci 9:25–37

Kikuchi E (1986) Contribution of the polychaete, *Neanthes japonica* (Izuka), to the oxygen uptake and carbon dioxide production of an intertidal mud-flat of the Nanakita River Estuary, Japan. J Exp Mar Biol Ecol 97:81–93

Kikuchi E (1998) Life history and dispersal pattern of the polychaete worm *Neanthes japonica* (Izuka) in the Nanakita River Estuary, Miyagi Prefecture. Jpn J Limnol 59:125–146

Kikuchi E, Yasuda K (2006) Comparison of the life cycles of two sympatric estuarine polychaetes, *Hediste diadroma* and *H. atoka* (Polychaeta: Nereididae), in the Nanakita River estuary, northeastern Japan. Limnology 7:103–115

Lee J-H, Je J-G, Choi J-W (1992) Taxonomical review of *Perinereis aibuitensis* Grube, 1878 (Nereidae: Polychaeta) in Korea. Korean J Syst Zool 8:1–10

Leitão A, Carvalho S, Ben-Hamadou R et al (2010) Cytogenetics of *Hediste diversicolor* (Annelida: Polychaeta) and comparative karyological analysis within Nereididae. Aquat Biol 10:193–200

Lipari R, Vitturi R, Badalamenti F (1994) Cariotipo e organizzatori nucleolari (NORs) in *Perinereis macropus* (Claparede, 1870) (Annelida, Polychaeta). Biol Mar Mediterr 1:361–362

Marenzeller E (1879) Südjapanische Anneliden I. Denkschriften Kaiserlichen Akad Wiss Wien Math Naturwiss KI 41:109–154, pls. 1–6

McLusky DS, Elliott M (2004) The estuarine ecosystem. Ecology, threats, and management, 3rd edn. Oxford University Press, New York

Miura T (1990) *Nicon sinica* WU and SUN, 1979, a newly recorded polychaete from Japan. Benthos Res (Bull Jpn Assoc Benthol) 38:11–17

Miura T (2000) Annelida. In: Aoki J et al (eds) Systematic zoology: supplement. Nakayama Shoten, Tokyo, pp 158–167 (in Japanese)

Miyoshi S (1939) Swarming of *Ceratocephale osawai* in Hinuma. Bot Zool 7:2017–2024 (in Japanese)

Moore JP (1903) Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea. Proc Acad Nat Sci Phila 55:401–490

Nishi E (2003) Occurrence of *Namanereis littoralis* (Grube) species group (Nereidae) in Tokyo Bay (Annelida: Polychaeta). Nat Hist Rep Kanagawa 24:37–38 (in Japanese with English summary)

Nishi E (2005) Invasive marine and brackish water invertebrates in Kanagawa Prefecture. Actinia (Yokohama Nat Univ) 16:25–29 (in Japanese with English summary)

Nishi E, Kato T (2004) Introduced and globally invaded polychaetous annelids. Jpn J Benthol 59:22–44 (in Japanese with English summary)

Nishi E, Tanaka K (2011) Phylum Annelida (Classes Polychaeta and Myzostomida): a catalogue of Akira Izuka's type and non-type polychaete collection in the University Museum, the University of Tokyo. In: Ueshima R (ed) Catalogue of invertebrate collection deposited in the Department of Zoology, the University Museum, the University of Tokyo (3). Material Reports, No. 90. The University Museum, The University of Tokyo, Tokyo, pp 1–57

Nishizawa R, Sato M, Furota T, Tosuji H (2014) Cryptic invasion of northeast Pacific estuaries by the Asian polychaete, *Hediste diadroma* (Nereididae). Mar Biol 161:187–194

Okuda S (1933) Some polychaete annelids used as bait in the Inland Sea. Annot Zool Jpn 14:243–253, 2 pls

Okuda S (1938) Polychaetous annelids from the vicinity of the Mitsui Institute of Marine Biology. Jap J Zool 8:75–105

Okuda S (1939) Annelida Polychaeta in Onagawa Bay and its vicinity. II. Polychaeta Errantia with some addenda of Polychaeta Sedentaria. Rep Tohoku Imp Univ 14:219–244

Olive PJW (1983) Annelida—Polychaeta. In: Adiyodi KG, Adiyodi RG (eds) Reproductive biology of invertebrates, vol I, Oogenesis, oviposition, and oosorption. Wiley, Chichester, pp 357–422

Paik E-I (1973) The polychaetous annelids in Korea (II). Description of *Nectoneanthes latipoda,* sp. nov. Bull Korean Fish Soc 6:81–84

Paik E-I (1989) Illustrated encyclopedia of fauna & flora of Korea, vol 31, Polychaeta. Ministry of Education, Republic Korea, Seoul (in Korean)

Park TS, Kim W (2007) A taxonomic study on *Perinereis nuntia* species group (Polychaeta: Nereididae) of Korea. Korean J Syst Zool 23:75–85

Pesch GG, Pesch CE (1980) Chromosome complement of the marine worm *Neanthes arenaceodentata* (Polychaeta: Annelida). Can J Fish Aquat Sci 37:286–288

Pesch GG, Pesch CE, Mueller C (1988) Chromosome complements from two populations of the marine worm *Neanthes arenaceodentata* (Annelida: Polychaeta). Ophelia 28:163–167

Pettibone MH (1971) Revision of some species referred to *Leptonereis*, *Nicon*, and *Laeonereis* (Polychaeta: Nereididae). Smithson Contrib Zool 104:1–53

Riisgård HU (1991) Suspension feeding in the polychaete *Nereis diversicolor*. Mar Ecol Prog Ser 70:29–37

Riisgård HU (1994) Filter-feeding in the polychaete *Nereis diversicolor*: a review. Neth J Aquat Ecol 28:453–458

Rouse GW, Pleijel F (2001) Polychaetes. Oxford University Press, New York

Saito H, Niwa N, Kawai K, Imabayashi H (2011) Current state of aquatic animals sold as sport fishing bait in Western Japan. Bull Hiroshima Univ Mus 3:45–57 (in Japanese with English summary)

Saito H, Kawai K, Umino T et al (2014) Fishing bait worm supplies in Japan in relation to their physiological traits. Mem Mus Victoria 71:279–287

Sato M (1999) Divergence of reproductive and developmental characteristics and speciation in *Hediste* species group. Hydrobiologia 402:129–143

Sato M (2004) Diversity of polychaetes and environments in tidal flats: a study on the *Hediste* species group (Nereididae). Fossils 76:122–133 (in Japanese with English summary)

Sato M (2006) Diversity of polychaetes in tidal flats. Global Environ Res 11:191–206 (in Japanese)

Sato M (2010) Anthropogenic decline of the peculiar fauna of estuarine mudflats in Japan. Plankton Benthos Res 5(suppl):202–213

Sato M (2012) *Ceratonereis (Composetia)* sp. In: Japanese Association of Benthology (ed) Threatened animals of Japanese tidal flats: Red Data Book (RDB) of seashore benthos. Tokai University Press, Hatano, p 223 (in Japanese)

Sato M (2013) Resurrection of the genus *Nectoneanthes* Imajima, 1972 (Nereididae, Polychaeta), with redescription of *Nectoneanthes oxypoda* (Marenzeller, 1879) and description of a new species, comparing them to *Neanthes succinea* (Leuckart, 1847). J Nat Hist 47(1, 2):1–50

Sato M, Ikeda M (1992) Chromosome complements of two forms of *Neanthes japonica* (Polychaeta, Nereididae) with evidence of male-heterogametic sex chromosomes. Mar Biol 112:299–307

Sato M, Koh C-H (2004) Biological richness of the Asian tidal flats and its crisis by human impacts. In: Hong S-K et al (eds) Ecological issues in a changing world. Status, response and strategy. Kluwer, Dordrecht, pp 135–155

Sato M, Kubo A (2009) New records of a nereidid polychaete, *Leonnates persicus* from Japan, Korea and Thailand, with redescription of the holotype. Zool Sci 26:798–803

Sato M, Masuda Y (1997) Genetic differentiation in two sibling species of the brackish-water polychaete *Hediste jaoinica* complex (Nereididae). Mar Biol 130:163–170

Sato M, Nakashima A (2003) A review of Asian *Hediste* species complex (Nereididae, Polychaeta) with descriptions of two new species and a redescription of *Hediste japonica* (Izuka, 1908). Zool J Linn Soc 137:403–445

Sato M, Osanai K (1983) Sperm reception by an egg microvillus in the polychaete, *Tylorrhynchus heterochaetus*. J Exp Zool 227:459–469

Sato M, Sattmann H (2009) Extirpation of *Hediste japonica* (Izuka, 1908) (Nereididae, Polychaeta) in central Japan, evidenced by a museum historical collection. Zool Sci 26:369–372

Sato M, Tsuchiya M (1987) Reproductive behavior and salinity favorable for early development in two types of the brackish-water polychaete *Neanthes japonica* (Izuka). Benthos Res 31:29–42

Sato M, Tsuchiya M (1991) Two patterns of early development in nereidid polychaetes keying out to *Neanthes japonica* (Izuka). Ophelia Suppl 5:371–382

Sato M, Ebihara T, Kubo A et al (2013) Diversity of nereidid polychaete species in Asian estuaries. In: Abstracts of the International Conference on Oceanography and Sustainable Marine Production: a challenge of managing marine resources in a changing climate (ICOSMaP 2013). The Zenith Hotel, Kuantan, Pahang, Malaysia, 28–30 October 2013

Sato M, Ebihara, T, Kojima S et al (2014) Systematics of two undescribed *Composetia* species (Polychaeta: Nereididae) collected from estuaries in the Ryukyu Arc, southern Japan and Songkhla Lagoon, southern Thailand. In: Abstracts of the 2nd Asian Marine Biology Symposium (AMBS 2014). Ramada Plaza Jeju Hotel, Jeju, Korea, 1–4 October 2014

Sato-Okoshi W, Abe H, Okoshi K et al (2015) Harmful shell borers, *Polydora* species (Polychaeta: Spionidae), from commercially important mollusk shells in East Asia and Australia. In:

Ceccaldi H-J et al (eds) Marine productivity: perturbations and resilience of socio-ecosystems. Springer International, Cham, pp 31–41

Sayama M, Kurihara Y (1983) Relationship between burrowing activity of the polychaetous annelid *Neanthes japonica* (Izuka) and nitrification-denitrification processes in the sediments. J Exp Mar Biol Ecol 72:233–241

Scaps P (2002) A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O.F. Müller) (Annelida: Polychaeta). Hydrobiologia 470:203–218

Scaps P, Demuynck S, Lepretre A, Grumiaux F (2001) Electrophoretic heterogeneity in *Hediste diversicolor* (Annelida: Polychaeta) within and between estuaries in northern France. Vie Milieu 51:99–111

Schroeder PC, Hermans CO (1975) Annelida: Polychaeta. In: Giese AC, Pearse JS (eds) Reproduction of marine invertebrates, vol III. Academic Press, New York, pp 1–213

Smith RI (1950) Embryonic development in the viviparous nereid polychaete, *Neanthes lighti* Hartman. J Morphol 87:417–466

Smith RI (1958) On reproductive pattern as a specific characteristic among nereid polychaetes. Syst Zool 7:60–73

Smith RI (1964) On the early development of *Nereis diversicolor* in different salinities. J Morphol 114:437–464

Smith RI (1977) Physiological and reproductive adaptations of *Nereis diversicolor* to life in the Baltic Sea and adjacent waters. In: Reish DJ, Fauchald K (eds) Essays on polychaetous annelids, in memory of Dr. Olga Hartman. Allan Hancock Foundation, University of Southern California, Los Angeles, pp 373–390

Struck TH, Paul C, Hill N et al (2011) Phylogenomic analyses unravel annelid evolution. Nature (Lond) 471:95–98

Tanaka M (2016) First record of *Perinereis suluana* (Annelida, Nereididae) from Oura Bay, Okinawa Island, Ryukyu Islands, Japan. Fauna Ryukyuana 29:5–13

The Ecological Society of Japan (ed) (2002) Handbook of alien species in Japan. Chijinshokan, Tokyo (in Japanese with English summary)

Tittensor DP, Mora C, Jetz W et al (2010) Global patterns and predictors of marine biodiversity across taxa. Nature (Lond) 466:1098–1103

Toba Y, Sato M (2013) Filter-feeding behavior of three Asian *Hediste* species (Nereididae, Polychaeta). Plankton Benthos Res 8:159–165

Tosuji H, Furota T (2016) Molecular evidence for the expansion of the Asian cryptic invader *Hediste diadroma* (Nereididae: Annelida) into the northeast Pacific habitats of the native *H. limnicola*. Zool Sci 33:162–169

Tosuji H, Sato M (2006) Salinity favorable for early development and gamete compatibility in two sympatric estuarine species of the genus *Hediste* (Polychaeta: Nereididae) in the Ariake Sea, Japan. Mar Biol 148:529–539

Tosuji H, Sato M (2010) Genetic evidence for parapatric differentiation of two forms of the brackish-water nereidid polychaete *Hediste atoka*. Plankton Benthos Res 5(suppl):242–249

Tosuji H, Sato M (2012) A simple method to identify *Hediste* sibling species (Polychaeta: Nereididae) using multiplex PCR amplification of the mitochondrial 16S rRNA gene. Plankton Benthos Res 7:195–202

Tosuji H, Miyamoto J, Hayata Y, Sato M (2004) Karyotyping of female and male *Hediste japonica* (Polychaeta, Annelida) in comparison with those of two closely related species, *H. diadroma* and *H. atoka*. Zool Sci 21:147–152

Tosuji H, Togami K, Miyamoto J (2010) Karyotypic analysis of the hermaphroditic viviparous polychaete, *Hediste limnicola* (Polychaeta: Nereididae): possibility of sex chromosome degeneration. J Mar Biol Assoc UK 90:613–616

Tsuchiya M, Kurihara Y (1979) The feeding habits and food sources of the deposit-feeding polychaete, *Neanthes japonica* (Izuka). J Exp Mar Biol Ecol 36:79–89

Uchida H (1990) Vermiform animals. In: Picture book of organisms under the Sea of Okinawa, vol 11. The Southern Press, Naha, pp 16–85 (in Japanese)

Uchida H, Tanase H, Kubota S (2009) An extraordinarily large specimen of the polychaete worm *Eunice aphroditois* (Pallas) (Order Eunicea) from Shirahama, Wakayama, central Japan. Kuroshio Biosph 5:9–15, 1 pl

Virgilio M, Fauvelot C, Costantinif F, Abbiati M, Backeljau T (2009) Phylogeography of the common ragworm *Hediste diversicolor* (Polychaeta: Nereididae) reveals cryptic diversity and multiple colonization events across its distribution. Mol Ecol 18:1980–1994

Weinberg JR, Starczak VR, Mueller C, Pesch GC, Lindsay SM (1990) Divergence between populations of a monogamous polychaete with male parental care: premating isolation and chromosome variation. Mar Biol 107:205–213

Weinberg JR, Starczak VR, Jörg D (1992) Evidence for rapid speciation following a founder event in the laboratory. Evolution 46:1214–1220

Wilson RS (1988) Synonymy of the genus *Nectoneanthes* Imajima, 1972, with *Neanthes* Kinberg, 1866 (Polychaeta: Nereididae). Proc Biol Soc Wash 101:4–10

Wonham MJ, Carlton JT (2005) Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. Biol Invasions 7:369–392

Wu S-K (1967) The nereid worms of Taiwan. Bull Inst Zool Acad Sin 6:47–76

Wu BL, Sun RP (1979) Revision of the genera *Nicon* and *Rullierinereis*, with description of a new genus *Sinonereis* (Polychaeta: Nereidae). Ocean Select 2:95–112

Wu B, Sun R, Yang D (1985) The Nereidae (polychaetous annelids) of the Chinese coast. Springer/China Ocean Press, Beijing (first published in 1981 in Chinese)

Yamamoto T (1947) The optimum salinity for fertilization and development of a brackish-water polychaete, *Tylorrhynchus heterochaetus*. Physiol Ecol (Kyoto) 1:79–88 (in Japanese)

Yamanishi R, Sato M (2007) Annelida, polychaeta. In: Iijima A (ed) The 7th national survey on the natural environment: shallow sea survey (Tidal flats). Biodiversity Center, Nature Conservation Bureau, Ministry of the Environment, Fuji-yoshida (Yamanashi), pp 182–192 (in Japanese)

Zheng J, Wang M, Sun X, Zhou Z (1992) Karyotype studies on *Perinereis nuntia* (Savigny, 1818). J Ocean Univ Qingdao 22:102–106 (in Chinese with English summary)

Chapter 20
The Echiura of Japan: Diversity, Classification, Phylogeny, and Their Associated Fauna

Ryutaro Goto

Abstract Echiurans (spoon worms) are marine invertebrates that have a sausage-shaped unsegmented body with an extensible spoon-like proboscis. Most species live inside burrows in soft sediments. They have been classified as a separate phylum, but recent molecular phylogenetic and phylogenomic studies have consistently suggested that they are derived annelids that lost segmentation. This chapter introduces the classification and phylogeny of echiurans and provides a checklist of echiurans and their symbiotic animals in Japan. Echiurans have traditionally been grouped into three orders: Echiuroinea (with Echiuridae, Thalassematidae, and Bonelliidae), Xenopneusta (with Urechidae), and Heteromyota (with Ikedidae). Recent molecular phylogenetic analyses recover only two groups that contain sexually monomorphic (Echiuridae, Urechidae, and Thalassematidae) and sexually dimorphic species (Bonelliidae and Ikedidae), respectively. The echiuran fauna of Japan comprises 5 families, 19 genera, and 34 species, including 5 thalassematid species newly reported herein. The family Thalassematidae contains 20 species in 6 genera; Bonelliidae contains 10 species in 9 genera; Urechidae and Echiuridae are represented by a single species each (*Urechis unicinctus* and *Echiurus echiurus*, respectively); and Ikedidae contains 2 species, (*I. taenioides* and *Ikeda* sp. 1). One genus (*Acanthohamingia*) and 11 described species are known only from Japan. At least 29 commensal species have been collected from 12 species of host echiurans in Japan, including bivalves (7 species), gastropods (3 species), snapping shrimps (4 species), crabs (5 species), polychaetes (mainly scale worms) (7 species), and copepods (1 species). In addition, unidentified entoprocts are also found from thalassematid burrows.

Keywords Annelida • Burrow • Classification • Commensalism • Dwarf male • Echiura • Phylogeny • Sexual dimorphism • Spoon worm • Symbiosis

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20.1 Introduction

Echiurans, commonly known as spoon worms, are marine invertebrates that have a sausage-shaped unsegmented body with a highly extensible spoon-like proboscis. Most species live in burrows in soft sediments, although some occur within crevices in hard substrata (Fisher 1946; Stephen and Edmonds 1972; Jumars et al. 2015). The shape and depth of the burrows differ among species (Ditadi 1982). Burrows of large echiurans host a remarkable variety of symbionts, mostly commensals (Anker et al. 2005; Goto and Kato 2012).

Approximately 165 species of echiurans have been recorded from all the depth zones of all oceans (Biseswar 2009, 2010, 2012). Echiurans were originally included in Annelida (Sedgwick 1898). However, because of embryological and morphological evidence, they were separated as an independent phylum (Newby 1940). Nevertheless, recent molecular phylogenetic and phylogenomic studies consistently suggest that echiurans are derived annelids that secondarily lost segmentation (McHugh 1997; Struck et al. 2007, 2011; Kvist and Siddall 2013; Weigert et al. 2014), constituting a sister group to Capitellidae (Struck et al. 2007, 2011; Weigert et al. 2014). Thus, echiurans are currently ranked as a subgroup of the phylum Annelida again. Ruggiero et al. (2015) treated them as a subclass of Annelida.

Among echiurans, five subgroups (Echiuridae, Thalassematidae, Urechidae, Bonelliidae, and Ikedidae) have been recognized (DattaGupta 1976; Edmonds 2000; Ruppert et al. 2004), although Echiuridae and Thalassematidae are sometimes included within the same family (Stephen and Edmonds 1972). These subgroups are separated into two or three orders (Stephen and Edmonds 1972; Nishikawa 2002). However, recent molecular phylogenetic analyses suggest that the previous order-level classification does not reflect echiuran phylogenetic relationships and thus should be revised (Goto et al. 2012; Lehrke 2012).

Feeding mode differs among echiuran subgroups (Jumars et al. 2015). Most echiurans, including Thalassematidae, Echiuridae, Bonelliidae, and Ikedidae, are deposit feeders and collect sediments from around their burrows with their extensible proboscis (Chuang 1962; Jaccarini and Schembri 1977; Jumars et al. 2015). The shape and length of the proboscis vary among species, probably as the result of specialization for different modes of deposit feeding. On the other hand, members of Urechidae are filter feeders, using a peculiar mucous net to capture food (Fisher and MacGinitie 1928). Members of this family have a highly reduced proboscis and modified cloaca that are considered to be adaptations for filter feeding (MacGinitie and MacGinitie 1968).

Reproductive mode also differs among echiuran subgroups (Edmonds 2000). Bonelliid echiurans are well known as an example of extreme sexual dimorphism involving dwarf males (Edmonds 2000). In Bonelliidae, the small, ciliated males live inside the female body (usually in the gonoducts) and perform internal fertilization. Ikedidae may also possess dwarf males (Nishikawa 2002). Bonelliidae has high species diversity from abyssal to hadal zones (Ruppert et al. 2004). Thus, Zenkevitch (1966) and Goto et al. (2013) hypothesized that extreme sexual dimorphism may have originated as an adaptation to deep-sea environments. On the other hand, members of the other echiuran families (i.e., Echiuridae, Urechidae, Thalassematidae) do not show marked sexual dimorphism (i.e., males and females are similar in size) and perform external fertilization (Edmonds 2000).

The purpose of this chapter is to introduce the recent progress of molecular phylogenetic analyses of echiurans and to reevaluate the diversity of echiurans and their symbiotic animals in Japan. Several comprehensive reviews of Japanese echiurans (Satô 1939; Nishikawa 1992) and their symbiotic animals (Anker et al. 2005; Itani 2008) have previously been assembled. However, information on Japanese echiurans and their symbiotic animals has increased dramatically in recent years (Nishikawa 2002, 2004; Anker 2012; Goto et al. 2011, 2012, 2013, 2016a, b; Goto and Kato 2012; Goto 2016; Tanaka and Nishikawa 2013; Abe et al. 2014; Tanaka et al. 2014; Anker et al. 2015; Komai 2015). Thus, this is a good opportunity to update and reorganize our knowledge of Japanese echiurans and their symbiotic species.

20.2 Classification and Phylogeny

Echiurans have traditionally been classified into three orders: Echiuroinea Bock, 1942 (with Echiuridae Quatrefages, 1847 and Bonelliidae Lacaze-Duthiers, 1858), Xenopneusta Fisher, 1946 (with Urechidae Monro, 1927), and Heteromyota Fisher, 1946 (with Ikedidae Bock, 1942) (Stephen and Edmonds 1972) (Table 20.1a). The family Echiuridae is further separated into two subfamilies: Echiurinae Quatrefages, 1847 and Thalassematinae Forbes and Goodsir, 1841 (Table 20.1a).

The order Heteromyota was established for *Ikeda taenioides* based on muscle arrangements that are distinct from those in other echiurans (Fisher 1946). However, further examination of the musculature in this species by Nishikawa (2002) revealed that the muscle layer arrangement is not distinct. Thus, Nishikawa (2002) abolished the order Heteromyota and the family Ikedidae, transferring its sole genus *Ikeda* to Echiuridae sensu Stephen and Edmonds (1972). Thus, in the revised classification, echiurans comprised two orders: Echiuroinea (with Echiuridae and Bonelliidae) and Xenopneusta (with Urechidae) (Nishikawa 2002) (Table 20.1b).

Goto et al. (2013) performed a molecular phylogenetic analysis using four genes (18S rRNA, 28S rRNA, COI, and H3) obtained from members of the five echiuran subgroups: Echiuridae (Echiurinae sensu Stephen and Edmonds, 1972), Thalassematidae (Thalassematinae sensu Stephen and Edmonds, 1972), Bonelliidae, Ikedidae, and Urechidae. Maximum-likelihood and Bayesian analyses suggest that echiurans are divided into two major clades: (Echiuridae, Urechidae, and Thalassematidae) and (Bonelliidae and Ikedidae) (Fig. 20.1). The two major clades can be distinguished morphologically by sexual dimorphism with dwarf males (presence or absence), arrangement of gonoducts (paired or unpaired), and anal vesicles (branched or unbranched) (Goto et al. 2013). Within the former major

Table 20.1 Comparison of the three classification systems of Echiura

(a) Stephen and Edmonds (1972)	(b) Nishikawa (2002)	(c) Ruppert et al. (2004), this study
Order Echiuroinea	Order Echiuroinea	Family Echiuridae
Family Echiuridae	Family Echiuridae	Family Urechidae
Subfamily Echiurinae	Subfamily Echiurinae	Family Thalassematidae
Subfamily Thalassematinae	Subfamily Thalassematinae	Family Bonelliidae
Family Bonelliidae	Family Bonelliidae	Family Ikedidae
Order Xenopneusta	Order Xenopneusta	
Family Urechidae	Family Urechidae	
Order Heteromyota		
Family Ikedaidae		

clade, Echiuridae and Urechidae form a monophyletic group (Fig. 20.1). These two families share the character of having rings of anal chaetae surrounding the posterior end of the trunk, which is probably a synapomorphy for this clade (Goto et al. 2013), although, except for this, they are different in many aspects (such as proboscis shape, cloaca structure, vascular system, and feeding mode) (Ruppert et al. 2004).

Lehrke (2012) also constructed a molecular phylogeny of echiurans based on analyses of 18S rRNA, 16S rRNA, and COI genes. Similar to Goto et al. (2013), her phylogenetic tree supported (1) the monophyly of Bonelliidae and Ikedidae and (2) a sister group relationship of Echiuridae and Urechidae. However, the topology provided by Lehrke (2012) is different from that of Goto et al. (2013) in the following points: (1) the Echiuridae + Urechidae clade is sister to the Bonelliidae + Ikedidae clade, and (2) Thalassematidae is not monophyletic. This latter is probably because of the limited number of taxa and genes used by Lehrke (2012).

The results of molecular phylogenetic analyses in Lehrke (2012) and Goto et al. (2013) are not congruent with the previous order-level classification. For example, the order Echiuroinea (with Echiuridae, Thalassematidae, and Bonelliidae) is polyphyletic in resultant trees (Fig. 20.1). In addition, Urechidae, which belongs to its own order (Xenopneusta), was nested within two families belonging to the order Echiuroinea. Furthermore, *Ikeda*, which was assigned to the family Echiuridae sensu Stephen and Edmonds (1972) (Nishikawa, 2002), formed a monophyletic group with Bonelliidae.

The classification used in this chapter is shown in Table 20.1c; the family-level classification is similar to Ruppert et al. (2004). Echiuridae is restricted to the genus *Echiurus* and a number of *Thalassema*-like echiurans are placed in Thalassematidae. Although Ikedidae was abolished by Nishikawa (2002), it is morphologically distinct, because its members have (1) a larger number of gonoducts than all the other echiurans, (2) a huge body, and (3) a peculiarly colored proboscis (Fig. 20.2s, t; Ikeda 1907; Bock 1942; DattaGupta and Menon 1976; Lehrke 2012). Thus, this family is retained in the classification employed in this chapter.

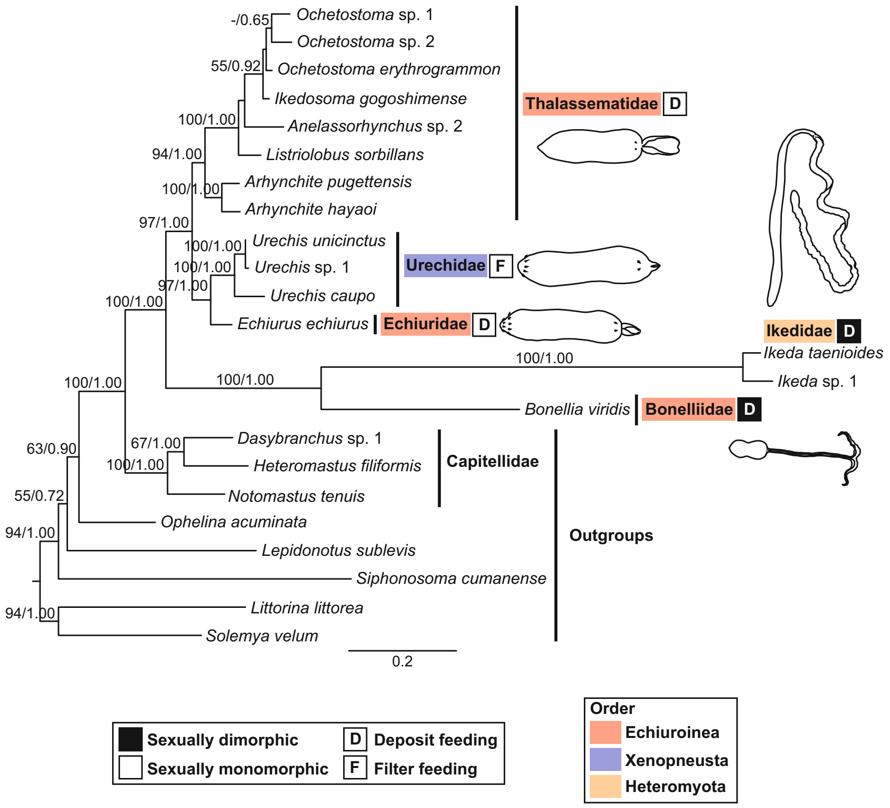

Fig. 20.1 Maximum-likelihood tree of echiuran worms based on a combined dataset of 18S, 28S, H3, and COI gene regions. *Numbers* above branches indicate maximum-likelihood bootstrap support values followed by Bayesian posterior probabilities. The colors of the *boxes* to the right of the family names indicate whether the family is sexually dimorphic (*black*) or monomorphic (*white*). The *capital letters* in the boxes indicate the feeding mode of the family, i.e., deposit feeding (*D*) or filter feeding (*F*). The colors shading the family names indicate the order to which the family belongs, as defined by Stephen and Edmonds (1972) (This figure is modified from Goto et al. 2013). *Arhynchite hayaoi* and *Anelassorhynchus* sp. 2 in this figure correspond to *Thalassema owstoni* and *Ochetostoma* sp. 3 in Goto et al. (2013), respectively

20.3 Echiuran Fauna of Japan

20.3.1 Diversity of Japanese Echiurans

The Japanese Archipelago has a broad range of latitudes, including subpolar, temperate, and tropical zones. The shallow-water echiuran fauna transforms from north to south along different islands. In Hokkaido, the northern island of Japan, the cold-water species *Echiurus echiurus* (Pallas, 1766) (Echiuridae) lives in mud bottoms in the seagrass beds (Okuda 1946). *Arhynchite arhynchite* (Ikeda, 1924), the sole echiuran species with no proboscis, was collected from Hokkaido and the most northern part of Honshu Island (Ikeda 1924; Satô 1937a), although it has not been collected recently. *Urechis unicinctus* (Drasche, 1881) (Urechidae), which is a peculiarly shaped filter-feeding echiuran, lives on sandy coasts from subpolar to temperate latitudes (Satô 1931, 1937a, 1939). In the temperate zone of Honshu, the main island of Japan, *Ikedosoma gogoshimense* (Ikeda, 1904) (Thalassematidae), *Arhynchite hayaoi* Tanaka and Nishikawa, 2013 (Thalassematidae), and *Ikeda taenioides* (Ikeda, 1904) (Ikedidae) live in sand and mud flats (Ikeda 1904, 1907; Satô 1937a, 1939; Goto et al. 2011, 2016b; Tanaka and Nishikawa 2013). These three species are thought to be endemic to Japanese waters (Nishikawa 2012; Tanaka and Nishikawa 2013; Tanaka et al. 2014); the last species is the largest echiuran known (Nishikawa 2012). In the Ryukyu Islands, which include subtropical to tropical zones, *Ochetostoma erythrogrammon* Rüppell and Leuckart, 1828 (Thalassematidae) is common in gravelly coral sand flats (Goto and Kato 2012), and *Listriolobus sorbillans* (Lampert, 1883) (Thalassematidae) is often abundant in mudflats (Nishikawa 2004). Bonelliid species (e.g., *Bonellia*, *Ikedella*, and *Acanthobonellia*) live in dead coral rocks in the warm shallow waters of the Pacific Coast (Ikeda 1904, 1907; Satô 1939). On the other hand, deep-water species (mostly bonelliids) occur in mesopelagic to hadal zones (Ikeda 1904, 1908b, 1910; Zenkevitch 1958, 1964).

Iwaji Ikeda (1872–1922) described and recorded many shallow-water and some deep-water species from Japan (Ikeda 1904, 1905a, b, 1907, 1908a, b, 1910, 1924). Before the publication of his monograph *The Gephyrea of Japan* (Ikeda 1904), only one species, *Urechis unicinctus*, had been recorded from the waters around Japan. His contributions increased the number of echiuran species in Japan to 18. In addition, Zenkevitch (1957, 1958, 1964) reported some deep-sea echiurans from Japanese waters. Satô (1939) described *Listriolobus riukiuensis* Satô, 1939 from the Ryukyu Islands, which is now considered to be a junior synonym of *L. sorbillans* (Nishikawa 2004). Fisher (1946) described the bonelliid species *Acanthohamingia paradolum* (Fisher, 1946) (Bonelliidae) from Kagoshima Bay, which was later transferred to the genus *Amalosoma* (Fisher, 1948). Tanaka and Nishikawa (2013) described a new species of *Arhynchite* from the Seto Inland Sea, which had previously been misidentified as *Thalassema owstoni* by Satô (1934, 1939). Goto et al. (2013) reported several unidentified species (e.g., *Ikeda* sp. 1, *Ochetostoma* sp. 1, *O*. sp. 2) from southwestern Japan.

The echiuran fauna of Japan was previously reviewed by Satô (1939) and Nishikawa (1992). They both reported all the five echiuran families (Echiuridae, Urechidae, Thalassematidae, Bonelliidae, Ikedidae) from Japan (Satô 1939; Nishikawa 1992). Satô (1939) lists 19 species in 11 genera; Nishikawa (1992) lists 21 species in 16 genera. The echiuran fauna of the Indo-West Pacific, including Japan, was recently reviewed by Biseswar (2010), according to which 21 species in 16 genera are supposed to be known in Japan. Considering that about 165 species have been recorded and described from marine and brackish waters worldwide (Biseswar 2010), Japan contains about 13 % of the entire echiuran diversity.

Table 20.2 Echiuran fauna in Japan; the described species with asterisks (*) are only known from Japan

Family	Species	Depth	Distribution in Japan	Fig. 20.2	References
Echiuridae	*Echiurus echiurus* Fisher, 1948	Littoral	Hokkaido	a	Ikeda (1924) and Okuda (1946)
Urechidae	*Urechis unicinctus* (von Drasche, 1881)	Littoral	Hokkaido to Kyushu	b	Satô (1939)
Thalassematidae	*Arhynchite arhinchite* (Ikeda, 1924)*	Littoral	Northern part of Japan (Hokkaido, Aomori)	–	Ikeda (1924) and Satô (1939)
	Arhynchite hayaoi Tanaka & Nishikawa, 2013*	Littoral	Seto Inland Sea, Lake Hamana, Sagami Bay	c	Tanaka and Nishikawa (2013)
	Anelassorhynchus inansensis (Ikeda, 1904)	Littoral	Okinawa Island	–	Ikeda (1904)
	Anelassorhynchus mucosus (Ikeda, 1904)	Littoral	Sagami Bay	–	Ikeda (1904)
	Anelassorhynchus sabinus (Lanchester, 1905)	Littoral	Seto Inand Sea	–	Satô (1934)
	Anelassorhynchus sp. 1	Littoral	Amami-Oshima Island	e	Goto et al. (2013), this study
	Anelassorhynchus sp. 2	Littoral	Amami-Oshima Island, Okinawa Island	f	Anker (2012), this study
	Anelassorhynchus sp. 3	Littoral	Amami-Oshima Island	g	Goto (2016), this study
	Anelassorhynchus sp. 4	Littoral	Amami-Oshima Island	h	Goto (2016), this study
	Anelassorhynchus sp. 5	Littoral	Uwajima, Ehime, Shikoku	i	Goto (2016), this study
	Anelassorhynchus sp. 6	Littoral	Uwajima, Ehime, Shikoku	j	Goto (2016), this study
	Ikedosoma elegans (Ikeda, 1904)*	Littoral	Seto Inland Sea, Lake Hamana, Sagami Bay, Boso Peninsula, Ariake Sea?	o	Tanaka et al. (2014) and Komai (2015)
	Ikedosoma gogoshimense (Ikeda, 1904)*	Littoral	Seto Inland Sea, Sagami Bay, Yatsushiro Sea	n	Tanaka et al. (2014)

(continued)

Table 20.2 (continued)

Family	Species	Depth	Distribution in Japan	Fig. 20.2	References
	Listriolobus sorbillans (Lampert, 1883)	Littoral	Nansei Islands	p	Satô (1939) and Nishikawa (2004)
	Ochetostomae erythrogrammon Rüppell & Leuckart, 1828	Littoral	Nansei Islands and warm Pacific coasts	k	Satô (1939) and Goto and Kato (2012)
	Ochetostoma sp. 1	Littoral	Amami-Oshima Island	l	Goto et al. (2013)
	Ochetostoma sp. 2	Littoral	Amami-Oshima Island	m	Goto et al. (2013)
	Thalassema fuscum Ikeda, 1904 (probably *Arhynchite*)*	Littoral	Not described	–	Ikeda (1904)
	Thalassema owstoni Ikeda, 1904 (probably *Arhynchite*)*	~330 m	Uraga Channel, Tokyo Bay	–	Ikeda (1904)
	Thalassema sp. 1	~50 m	Amami-Oshima Island	d	Goto (2016), this study
Bonelliidae	*Acanthobonellia miyajimai* (Ikeda, 1904)	Littoral	Okinawa Island	–	Ikeda (1904) and Satô (1939)
	Acanthohamingia iijimai (Ikeda, 1908)*	~914 m	The basin (Okinose) of Sagami Bay	–	Ikeda (1908b)
	Acanthohamingia shiplei Ikeda, 1910*	~732 m	The basin (Okinose) of Sagami Bay	–	Ikeda (1910)
	Amalosoma paradolum (Fisher, 1946)*	~218 m	Kagoshima Gulf	–	Fisher (1946)
	Bonellia minor Marion & Rietsh, 1886	Littoral	Nansei Islands and warm Pacific coasts	q	Ikeda (1904) and Satô (1939)
	Choanostomellia filatovae Zenkevitch, 1964	~1693 m	Off northeastern Japan (39°45′N, 143°22′E)	–	Zenkevitch (1964)
	Ikedella misakiensis (Ikeda, 1904)	Littoral	Warm Pacific coasts	r	Ikeda (1904), Satô (1939), and Goto (2016)
	Jakobia birsteini Zenkevitch, 1958	6,150–8,100 m	Kurile–Kamchatka Trench	–	Zenkevitch (1958)

	Protobonellia mitsukurii Ikeda, 1908*	~549 m	The basin (Okinose) of Sagami Bay	–	Ikeda (1908a)
	Vitjazema ultraabyssalis (Zenkevitch, 1958)	5560–9700 m	Kurile-Kamchatka Trench	–	Zenkevitch (1958)
Ikedidae	*Ikeda taenioides* (Ikeda, 1904)*	Littoral	Kyushu (Kagoshima) to Honshu (Mutsu)	s	Ikeda (1904), Satô (1931), and Goto et al. (2016b)
	Ikeda sp. 1	Littoral	Ishigaki Island	t	Goto et al. (2013)

To reevaluate echiuran diversity in Japan, I reexamined the literature and referred to my unpublished data. These analyses revealed that at least 34 species in 19 genera of echiurans occur in Japanese waters (1 urechid, 1 echiurid, 2 ikedids, 10 bonelliids, and 20 thalassematids) (Table 20.2), including 5 species that are newly reported in this chapter. Of the 24 described species, 11 have been recorded only from Japan (Table 20.2). *Acanthohamingia*, which comprises two deep-sea bonelliids, is the sole genus endemic to Japan (Table 20.2). Overall, 26 of the 34 species are from intertidal and subtidal zones and 8 are from deeper zones. Of the 8 deep-sea species, *Thalassema owstoni* (Thalassematidae) was collected from about 330 m depth in the Uraga Channel (Ikeda 1904), five bonelliids were found in the mesopelagic zone (200–1000 m), and two bonelliids are known from abyssal to hadal zones (below 4000 m) (Table 20.2).

20.3.2 Description of Japanese Echiurans

The diversity of each echiuran subgroup in Japan is mentioned next in detail with brief morphological and ecological accounts.

20.3.2.1 Family Echiuridae Quatrefages, 1847

Echiuridae is represented by a single genus, *Echiurus* Guérin-Méneville, 1831, containing about four species. Echiurids are similar to thalassematids in appearance (Fig. 20.2a), but can be distinguished from the latter in having two rings of anal chaetae around the posterior end of the trunk (Fig. 20.2a). They have a grayish-brown trunk, covered by many rings of papillae; a post-pharyngeal diaphragm is present, separating the coelom into two parts; gonoducts occur in one to three pairs; gonostomal lips are not spirally coiled. They are usually found in shallow cold waters at high latitudes (Biseswar 2009, 2010, 2012), although Biseswar (1997) reported *E. echiurus* from the subtropical waters of southern Africa. Of the four congeners, only one species, *E. echiurus* (Fig. 20.2a), has been recorded from northern Japan (Hokkaido) (Okuda 1946; Nishikawa 2007; Goto et al. 2013).

20.3.2.2 Family Urechidae Monro, 1927

Urechidae is monotypic; the sole genus *Urechis* Seitz, 1907 includes four species. Urechids are moderate to very large in body size; up to 500 mm in *U. caupo* Fisher and MacGinitie, 1928. The proboscis is very much reduced; the body color is beige or orange; with one anal chaetae ring around the posterior end of the trunk; gonoducts occur in two to three pairs; gonostomal lips are spirally coiled; the vascular system is open; the distal part of the midgut is greatly enlarged and functions as a respiratory chamber (i.e., water lung). Species in *Urechis* perform

Fig. 20.2 The diversity of echiurans in Japanese waters. (**a**) *Echiurus echiurus*. (**b**) *Urechis unicinctus*. (**c**) *Arhynchite hayaoi*. (**d**) *Thalassema* sp. 1 (*upper*: individual A; *lower*: individual B). (**e**) *Anelassorhynchus* sp. 1. (**f**) *Anelassorhynchus* sp. 2 with the commensal shrimp *Athanopsis gotoi*. (**g**) *Anelassorhynchus* sp. 3. (**h**) *Anelassorhynchus* sp. 4. (**i**) *Anelassorhynchus* sp. 5. (**j**) *Anelassorhynchus* sp. 6. (**k**) *Ochetostoma erythrogrammon*. (**l**) *Ochetostoma* sp. 1. (**m**) *Ochetostoma* sp. 2. (**n**) *Ikedosoma gogoshimense*. (**o**) *Ikedosoma elegans*. (**p**) *Listriolobus sorbillans*. (**q**) *Bonellia minor*. (**r**) *Ikedella misakiensis*. (**s**) *Ikeda taenioides*. (**t**) *Ikeda* sp. 1. [Photograph credits: R. Goto (**d**–**h**, **k**–**n**, **p**, **s**, **t**); Goto et al. 2013 (**b**, **c**, **t**); H. Ishikawa (**h**, **j**, **q**, **r**); H. Kajihara (**a**); Tanaka et al. 2014 (**o**)]

filter feeding using a mucous net (Fisher and MacGinitie 1928; MacGinitie and MacGinitie 1968). Of the four congeners, only one species, *U. unicinctus* (Fig. 20.2b), has been recorded from Japan. This species lives in U-shaped burrows in the sand bottom of the intertidal and subtidal zones. This species was previously very common and abundant everywhere along the coast of Japan (Satô 1939). However, their abundance has seriously decreased because of habitat destruction (Nishikawa 2007, 2012). Swimming and stranding are observed during low tide during winter nights in northeastern Japan (Abe et al. 2014), a phenomenon that is suggested to represent reproductive swarming (Abe et al. 2014). Many commensals have been reported from the burrows (see Sect. 20.4).

20.3.2.3 Family Thalassematidae (Sensu Thalassematinae Forbes and Goodsir, 1841)

Thalassematidae includes about 80 species worldwide in 7 genera: *Arhynchite*, *Thalassema*, *Lissomyema*, *Ochetostoma*, *Listriolobus*, *Ikedosoma*, and *Anelassorhynchus*. Members of this family usually live in shallow waters from temperate to tropical zones (Ruppert et al. 2004). They lack anal chaetae without showing a marked sexual dimorphism; their body color is variously green, black, orange, red, and purple (Fig. 20.2c–p). Thalassematidae is the most species-rich echiuran subgroup from the intertidal zone of Japan; at least 20 species in all the genera except *Lissomyema* have been recorded (Table 20.2).

Thalassema Lamarck, 1801 includes about 23 species worldwide. Members in this genus have a well-developed proboscis; body wall outer longitudinal and inner oblique muscle layers are continuous and not grouped in bands or fascicles; gonoducts occur in one to two pairs; gonostomal lips are flap like without a stalk and not spirally coiled (Lehrke 2012). Ecology is largely unknown, but at least the type species *T. thalassemum* and its closely related species live in galleries and crevices in rocks (Fisher 1946). *Thalassema* is the oldest genus in this family. Many thalassematid species were originally described as a member of this genus and then transferred to other genera later established. However, *Thalassema* still includes not a few species that should be transferred to other genera. From Japan, 2 species, *T. owstoni* and *T. fuscum* (Ikeda, 1904), have been reported (Ikeda 1904). *Thalassema owstoni* has been known only from a single, damaged specimen collected from about 330 m depth in the Uraga Channel near Tokyo Bay (Ikeda 1904); the type locality of *T. fuscum* was not stated by Ikeda (1904), and the species has not been recorded since the original description. The detailed description and illustration of the two species by Ikeda (1904) suggest they actually belong to *Arhynchite* (e.g., continuous longitudinal musculature, one pair of gonoducts, and leaf-like gonostomal lips). The orange-yellowish body color and the trunk surface densely covered by prominent papillae in *T. fuscum* are similar to those in *A. hayaoi* (Tanaka and Nishikawa 2013). The funnel-shaped gonostomal lip of *T. owstoni* can be categorized into a leaf-like gonostomap lip as it has a broad part on the tip. It also has a short stalk on the base, similar to the gonostomal lip in *Arhynchite pugettensis* (Fisher 1949).

One species of *Thalassema* (Fig. 20.2d) was collected from depth of about 50 m in the Setouchi Channel between Amami Ōshima and Kakeromajima (Goto 2016). This species lives in the galleries of rocks formed by rock-boring bivalves *Gastrochaena*, similar to *T. thalassemum* (type species of the genus). A small, pinkish trunk (less than 1 cm even in mature individuals) has a highly extensible proboscis, which is about seven times longer than the trunk (Fig. 20.2d); the well-developed long proboscis is probably an adaptation to collect food particles from burrows in rocks, similar to *Bonellia* species; gonoducts occur in two pairs (Goto, unpublished data). Its appearance and anatomic characteristics are very similar to those of *T. thalassemum*.

Arhynchite Satô, 1937 contains about eight species worldwide. Body wall longitudinal and inner oblique layers of muscles are continuous and not grouped in bands or fascicles; gonoducts occur in one pair; gonostomal lips are leaf like, sometimes with a short stalk. *A. arhynchite* and *A. hayaoi* are distributed in Japan; they have not been recorded outside Japanese waters so far. *Arhynchite arhynchite* is the type species of this genus and has been known only from the northern part of Japan (Aomori and Hokkaido) (Ikeda 1924; Sato 1937a), although it has not been collected recently. *Arhynchite arhynchite* is distinct from all other echiurans in having no proboscis (Ikeda 1924). *Arhynchite hayaoi* (Fig. 20.2c) is common in sandy mud flats in the Seto Inland Sea and temperate Pacific coasts of eastern Japan (Tanaka and Nishikawa 2013). The proboscis in this species is easily detached from the trunk.

Ochetostoma Rüppell and Leuckart, 1828 is composed of about 30 species in the world, which accounts for nearly half the species diversity in Thalassematidae. The body wall longitudinal musculature is thickened into bands; oblique muscles are fasciculated; gonoducts occur in one to seven pairs; gonostomal lips are spirally coiled. From Japan, *Ochetostoma erythrogrammon* (Fig. 20.2k) and 2 unidentified species (Fig. 20.2l, m) have been recorded (Satô 1939; Goto et al. 2013). *Ochetostoma erythrogrammon* is common in gravelly sand flats in the Ryukyu Islands, living in shallow horizontal burrows (Goto and Kato 2012). Stephen and Edmonds (1972) and Biseswar (2010) erroneously listed *O. palense* (Ikeda, 1924) as if it was from Misaki, eastern Japan, but the species was actually described based on specimens from Palau (Ikeda 1924).

Ochetostoma sp. 1 (Fig. 20.2l) has a pale red-violet trunk; the proboscis is white without pigments; body wall longitudinal muscle bands are present only on the ventral side and the number is eight; gonoducts occur in three pairs (Goto, unpublished data). Only known from Chinoura, Kakeromajima, southwestern Japan (Goto et al., 2013).

Ochetostoma sp. 2 (Fig. 20.2m) has a trunk and proboscis fully covered by dark green papillae; the number of body-wall longitudinal muscle bands is 18. This species was collected from the shallow U-shaped burrows under rocks in gravelly sand flats at Edateku, Amami Ōshima (Goto et al. 2013) and Derikyonma, Kakeromajima (Goto, unpublished data), southwestern Japan.

Listriolobus Spengel, 1912 includes about eight species. Body wall longitudinal musculature is thickened into bands; inner oblique muscles are continuous; gonoducts occur in one to five pairs; gonostomal lips are spirally coiled. Only one species, *Listriolobus sorbillans* (Fig. 20.2p), has been recorded from Japan (Satô 1939; Nishikawa 1992). This species is often abundant in mudflats of the Ryukyu Islands (Nishikawa 2004). It lives in deep vertical burrows that have a single opening; it extends its long proboscis from the burrow entrance onto the mudflat surface for feeding; the proboscis often exceeds 1 m in length; extension and retraction of the proboscis on the mudflat leave radial lines that surround the burrow entrance (Goto, personal observation).

Ikedosoma Bock, 1942 includes three species, of which two are known in Japan. The body wall longitudinal musculature is thickened into bands; inner oblique muscles are continuous; gonoducts occur in three to seven pairs; gonostomal lips are spirally coiled. *Ikedosoma* may be distinguishable from *Listriolobus* in having a rectal caecum (Tanaka et al. 2014). *Ikedosoma gogoshimense* (Fig. 20.2n) and *I. elegans* (Ikeda, 1904) (Fig. 20.2o) may be endemic to Japan.

Ikedosoma gogoshimense is common in gravelly-sand or mudflats in the Seto Inland Sea (Goto et al. 2011) and has also been collected from the temperate Pacific coast of eastern Japan and the Yatsushiro Sea (Ikeda 1904; Tanaka et al. 2014). The burrow is L shaped with one entrance (Kawaguti 1968; Goto et al. 2011). Fecal pellets are typically scattered around the burrow entrance (Kawaguti 1968; Goto et al. 2011; Tanaka et al. 2014). The body surface of *I. gogoshimense* is covered by numerous dark-greenish spots. Kawaguti (1968) observed intracellular green algae on the body surface of *I. gogoshimense*. However, I have never detected the existence of such algae with florescence microscopy (Goto, unpublished data).

Ikedosoma elegans occurs in the Seto Inland Sea and temperate Pacific coast of eastern Japan (Ikeda 1904, 1907; Tanaka et al. 2014; Komai 2015). *Ikedosoma elegans* or its closely related species was also collected from Ariake Sea, western Japan (Komai 2015). It has a large reddish trunk (up to 210 mm) and long proboscis with greenish pigments (Tanaka et al. 2014).

Anelassorhynchus Annandale, 1922 includes about 17 species from the world oceans. Body wall longitudinal and inner oblique muscles are continuous; gonoducts occur in one to five pairs; gonostomal lips are spirally coiled. Three species, *A. sabinus* (Lanchester, 1905), *A. mucosus* (Ikeda, 1904), and *A. inansensis* (Ikeda, 1904), have been recorded from Japan. However, there have been no reliable records following the first report of each species.

Anelassorhynchus sabinus was described in Singapore (Lanchester 1905); the Japanese specimen was collected in the Seto Inland Sea (Satô 1934).

Anelassorhynchus mucosus was described from muddy shores of Moroiso near the Misaki Marine Laboratory (Ikeda 1904); it very closely resembles *I. gogoshimense* except for the body size and color (Ikeda 1904; Satô 1939). The body wall longitudinal muscle bands are less evident in young individuals of *I. gogoshimense*, and their body color is similar to that of *A. mucosus* in Ikeda (1904) (Goto, personal observation). Thus, I suspect that type specimens of *A. mucosus* may be young individuals of *I. gogoshimense*.

Anelassorhynchus inansensis was described based on a single specimen from a coral reef of Inanse in Okinawa Island, southwestern Japan (Ikeda 1904).

I reexamined the specimen of "*Ochetostoma* sp. 3" in Goto et al. (2013) to find that it actually represents a young individual of an unidentified species of *Anelassorhynchus* (Fig. 20.2e, herein referred to as 'sp. 1'). Anker (2012) reported *O. erythrogrammon* from Amami Ōshima as a host of the commensal snapping shrimp *Athanopsis gotoi* Anker, 2012. However, reexamination of this specimen revealed that it is also a member of *Anelassorhynchus* (Fig. 20.2f, 'sp. 2'). In addition, I herein report additional four unidentified species of *Anelassorhynchus* from Amami Ōshima and western Shikoku (Fig. 20.2g–j). In total, nine species of this genus occur in Japan (Table 20.2). Perhaps *Anelassorhynchus* is the most diverse thalassematid genus in Japan, although its diversity has not been recognized. Below I give brief morphological and ecological accounts for the six unidentified species of *Anelassorhynchus*.

Anelassorhynchus sp. 1 (Fig. 20.2e) has a black trunk; the proboscis is pale yellow with dirty blackish pigments, laterally expanded at apex so as to present a bilobed appearance; with three pairs of gonoducts; gonostomal lips are spirally coiled. It lives in horizontal burrows under rocks in gravelly sand flats. This form is morphologically similar to *A. inansensis* in fig. 22 of Ikeda (1904). However, it is different from *A. inansensis* in the following points: (1) body surface is not covered by dark greenish papillae and (2) lateral margins of the proboscis are not brown. *Ochetostoma* sp. 3, reported by Goto et al. (2013), is a young individual of this species. The body color changes from pale purple with dirty greenish pigments to black as they mature. Presently only known from the western parts of Amami Ōshima, southwestern Japan (Goto et al. 2013; this study).

Anelassorhynchus sp. 2 (Fig. 20.2f) has a pale purple trunk, uniformly spotted by blackish pigments; the proboscis is white in color without pigments; with two pairs of gonoducts; gonostomal lips are spirally coiled. It lives in horizontal burrows in gravelly sand flats; it hosts the commensal snapping shrimp *Athanopsis gotoi* (Fig. 20.3a) (Anker 2012). This form was misidentified as "*O. erythrogrammon*" by Anker (2012); it is different from *A. inansensis* in having no pigments on the proboscis. Only known from southwestern Japan (Amami Ōshima and the Okinawa Islands) (Anker 2012).

Anelassorhynchus sp. 3 (Fig. 20.2g) has a blackish trunk; the proboscis is white in color, with dirty grayish green pigments, laterally expanded at its apex so as to present a bilobed appearance; with two pairs of gonoducts; gonostomal lips are spirally coiled. It lives in horizontal burrows in gravelly sand flats. This form is closely related to *Anelassorhynchus* sp. 1 but different from *A. inansensis* in the color of the proboscis and the number of gonoduct pairs. Only known from Derikyonma, Kakeromajima, southwestern Japan (Goto 2016).

Anelassorhynchus sp. 4 (Fig. 20.2h) has a slender, black trunk; the proboscis is white in color, with slightly dark pigments, much shorter than the trunk; the trunk wall is thin; with three pairs of gonoducts; gonostomal lips are spirally coiled. It lives under rocks of gravelly intertidal flats, not having permanent burrows but

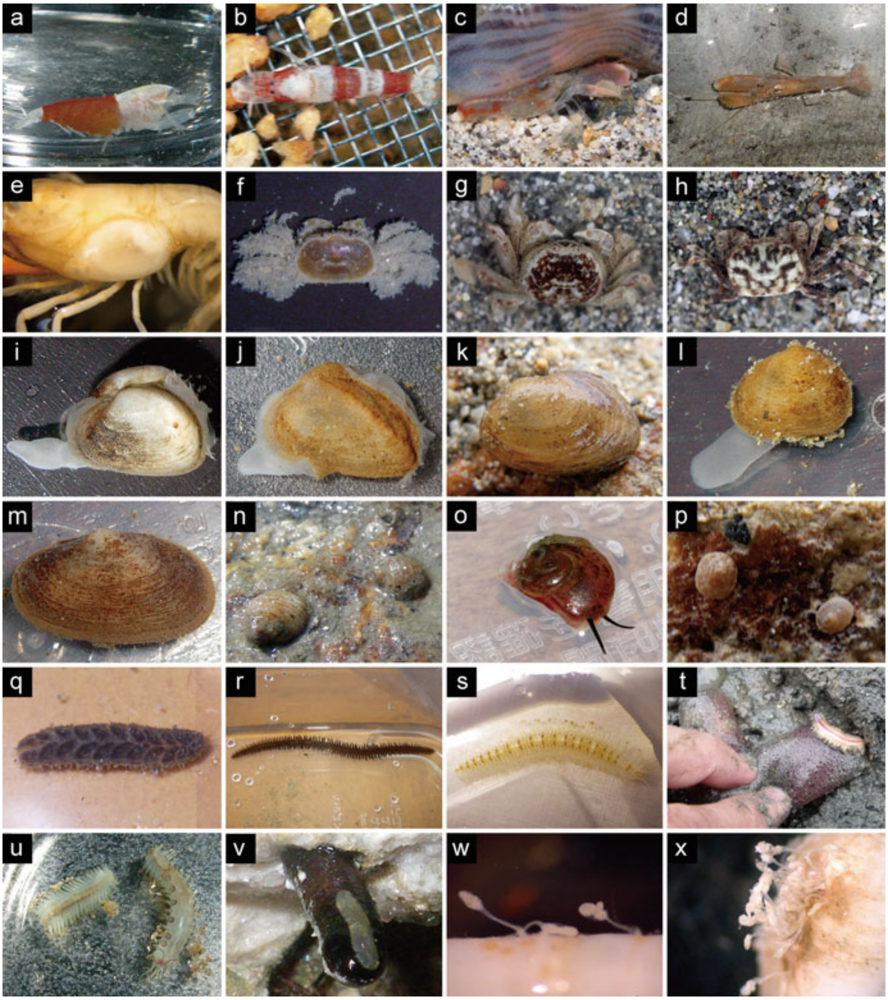

Fig. 20.3 Symbiotic animals associated with Japanese echiurans. (**a**) *Athanopsis gotoi*. (**b**) *Athanopsis brevirostris*. (**c**) *Alpheus barbatus*. (**d**) *Alpheus* cf. *barbatus*. (**e**) Lateral side of *A. barbatus* parasitized by an unidentified isopod. (**f**) *Mortensenella forceps*. (**g**) *Pseudopinnixa carinata*. (**h**) *Sestrostoma balssi*. (**i**) *Basterotia gouldi*. (**j**) *Basterotia carinata*. (**k**) *Basterotia* cf. *borbonica*. (**l**) *Byssobornia yamakawai*. (**m**) *Pseudopythina ochetostomae*. *(***n**) *Macromphalus tornatilis*. (**o**) *Sigaretornus* cf. *planus*. (**p**) *Phenacolepas* sp. 1. (**q**) *Lepidonotus* sp. 1. (**r**) Hesionidae sp. 1. (**s**) Polynoinae sp. 1. (**t**) Lepidonotinae sp. 1. (**u**) Lepidonotinae sp. 2. (**v**) An unidentified scale worm (Polynoidae sp. 1) on the trunk of *Bonellia minor*. (**w**) Entoprocts on the carapace of *A. barbatus*. (**x**) Entoprocts living on the shell of *B. gouldi*. Host echiuran species: *Anelassorhynchus* sp. 2 (**a**), *Ochetostoma erythrogrammon* (**b**, **c**, **e**, **j**–**l**, **p**–**r**, **w**), *O*. sp. 1 (**d**), *O*. sp. 2 (**u**), *Listriolobus sorbillans* (**f**, **k**, **m**, **o**, **s**), *Urechis unicinctus* (**g**, **h**), *Ikedosoma gogoshimense* (**i**, **n**, **t**, **x**), *Arhynchite hayaoi* (**i**, **n**), *Bonellia minor* (**v**). [Photograph credits: R. Goto (**a**, **c**–**f**, **i**–**m**, **p**–**x**), Goto and Kato 2012 (**b**), G. Itani (**g**, **h**), Y. Hamamura (**n**), Y. Kameda (**o**)]

actively moving in gravel. Presently only known from Uken, Amami Ōshima, southwestern Japan (Goto 2016).

Anelassorhynchus sp. 5 (Fig. 20.2i) has a grayish-purple trunk; the proboscis is whitish, with dark pigments; with two pairs of gonoducts; gonostomal lip is weakly coiled. It lives in shallow horizontal burrows in gravelly and sandy mudflats. Presently only known from Uwajima, Ehime Prefecture, Japan (Goto 2016).

Anelassorhynchus sp. 6 (Fig. 20.2j) has a reddish-violet trunk, uniformly covered with small papillae of a dirty green color; the shovel-shaped proboscis is yellowish orange in color, edged with brown on lateral margins that are serrated, especially when shrunken (Fig. 20.2j); with two pairs of gonoducts; gonostomal lips are spirally coiled. It lives in shallow horizontal burrows in gravelly and sandy mudflats. The ventral nerve cord is clearly visible when the body is expanded as similar to *A. inansensis* in fig. 22 of Ikeda (1904). The appearance of this form is similar to that of *A. inansensis*. Presently only known from Uwajima, Ehime Prefecture, Japan (Goto 2016).

20.3.2.4 Family Bonelliidae Lacaze-Duthiers, 1858

Bonellidae includes about 32 genera. The members exhibit extreme sexual dimorphism. The dwarf males usually live in the gonoducts of females. The proboscis is often bifid and is capable of great extension. Two anal vesicles are usually branched frequently. The body is often greenish because of the green pigment bonellin (Ruppert et al. 2004). Most genera are known only from deep waters. Shallow-water species in *Bonellia* and *Acanthobonellia* often live in the crevices of rocks or dead corals.

At least ten species in nine genera have been recorded from Japan. One genus (*Acanthohamingia*) and four species are endemic to Japan (Table 20.2). Three genera and three species, *Bonellia minor* Marion and Rietsh, 1886, *Acanthobonellia miyajimai* (Ikeda, 1904), and *Ikedella misakiensis* (Ikeda, 1904), have been recorded from the intertidal to subtidal zones. The proboscis of these three species is bifid. These three genera can be distinguished by the number of ventral chaetae (two in *Bonellia*, numerous in *Acanthobonellia*, absent in *Ikedella*). Nine species in five genera have been collected from deep bottoms in Japanese waters (Table 20.2). The proboscis of the deep-water species in Japan is not bifid and body color is varied (e.g., green, white, yellow, or yellowish red).

Bonellia Rolando, 1821 includes about nine species worldwide; the proboscis is bifid; two ventral chaetae are present; the trunk is greenish in color; a single gonoduct with a basally placed gonostome is present. *Bonellia minor* (Fig. 20.2q) has been recorded from the warm Pacific Coast of southwestern Japan (Ikeda 1904; Satô 1939; Kawaguti 1971). This species usually lives in dead corals or limestone. Kawaguti (1971) found algal symbionts on the body surface. *Bonellia minor* was originally described based on specimens collected in the Mediterranean Sea. Thus, '*B. minor*' in Japanese waters is likely to represent a different species. Actually, Ikeda (1904) noticed that the anal gland in *B. minor* differs among specimens from Japan and the Mediterranean Sea. In addition, according to the molecular analysis, '*B. minor*' from Okinawa Island includes at least two cryptic species (large and small species) (Goto 2016).

Ikedella Monro, 1972 includes about four species from the world; the proboscis is bifid; no ventral chaetae; a single gonoduct is present; the gonostome on a short stalk is situated near the distal end of the gonoduct. *Ikedella misakiensis* (Ikeda, 1904) has been recorded from the warm Pacific coast of Japan (Ikeda 1904; Satô 1939). This species was recently collected in shallow waters of Uwajima, Ehime, Japan (Goto 2016; Fig. 20.2r). The trunk of *I. misakiensis* is light grayish brown in color with numerous brownish spots. The proboscis is densely marked with bluish-black spots. A number of spine-like bodies project from the entire external surface of the worm. The gonoduct is nearly as long as the body.

Acanthobonellia Fisher, 1948 includes about three species worldwide; the proboscis is bifid; a single gonoduct is present; ventral chaetae are often numerous. *Acanthobonellia miyajimai* has been recorded from Okinawa Island, southern Japan (Ikeda 1904). The trunk is grayish brown. Proboscis is covered with black spots.

Acanthohamingia Ikeda, 1910 includes two species that are endemic to Japan. The proboscis is not bifid; ventral chaetae are numerous; the trunk is bright yellowish red or pale yellow in color. *Acanthohamingia ijimai* (Ikeda, 1908) was collected at 920 m depth outside Okinose in Sagami Bay, Japan (Ikeda 1908b), whereas *A. shiplei* Ikeda, 1910 was collected at 740 m depth in the basin (the Okinose) of Sagami Bay (Ikeda 1910).

Amalosoma Fisher, 1948 includes about three species; the proboscis is unknown; ventral chaetae are absent; with two gonoducts. *Amalosoma paradolum* (Fisher, 1946) was described based on a specimen collected at 218 m depth in Kagoshima Bay (Fisher 1946). Presently this species is only known from the type locality.

Choanostomellia Zenkevitch, 1964 includes about three species; the proboscis is not bifid and has a collar surrounding the basal part; ventral chaetae are absent; a single gonoduct with a basally placed gonostome is present. *Choanostomellia filatovae* Zenkevitch, 1964 was reported from 1693 m depth off northern Honshu Island (39°45′N, 143°22′E) (Zenkevitch 1964).

Jakobia Zenkevitch, 1958 includes about three species; the proboscis is not bifid; ventral chaetae are absent; a single gonoduct is present. *Jakobia birsteini* Zenkevitch, 1958 was collected at 6510–8100 m depth in the Kurile-Kamchatka Trench (Zenkevitch 1958).

Protobonellia Ikeda, 1908 includes about seven species; the proboscis is not bifid; two ventral chaetae are present; a single gonoduct with a basally placed gonostome is present. *Protobonellia mitsukurii* Ikeda, 1908 was collected at 554 m depth in Sagami Bay (Ikeda 1908a).

Vitjazema Zenkevitch, 1958 includes about four species; the proboscis is not bifid; two ventral chaetae are present; one pair of gonoducts is present; the skin is transparent and green in color. *Vitjazema ultraabyssalis* Zenkevitch, 1958 was collected from the Kurile–Kamchatka Trench at 5560–9970 m depth by Zenkevitch (1958).

20.3.2.5 Family Ikedidae Bock, 1942

Ikedidae is represented by a single genus, *Ikeda* Wharton, 1913, composed of two described species (*I. taenioides* and *I. pirotansis*). The body is very large in size and reddish in color; the proboscis is very long with a striped color pattern at the ventral side, but is not bifid; gonoducts with a distally placed gonostome are numerous.

Ikeda taenioides (Fig. 20.2s) and one undescribed species, *Ikeda* sp. 1 (Fig. 20.2t), have been recorded from Japan (Ikeda 1907; Goto et al. 2013, 2016b). *Ikeda taenioides* is known from intertidal to subtidal zones from Mutsu to Kyushu (Ikeda 1901, 1904, 1907; Satô 1931, 1937b; Goto et al. 2016b), whereas *Ikeda* sp. 1 is only known from intertidal zones in Ishigaki Island in the Ryukyu Islands (Goto et al. 2013). Both species live in very deep burrows in fine sand bottoms (Ikeda 1901, 1904, 1907; Goto et al. 2013, 2016b), extending its long proboscis from the burrow entrance onto the sediment bottom surface for feeding. The color pattern of the proboscis is different between *I. taenioides* and *Ikeda* sp. 1 (Fig. 20.2s, t): *I. taenioides* has black fine stripes on the proboscis (Fig. 20.2s) whereas *Ikeda* sp. 1 has numerous small black spots on the proboscis (Fig. 20.2t).

20.4 Symbiotic Animals Associated with Echiurans in Japan

The burrows of echiuran worms are inhabited by various commensal organisms that are well reviewed by Anker et al. (2005). Recently, many commensal animals have been discovered in Japanese waters (Goto et al. 2011, 2012, 2016a; Goto and Kato 2012; Anker 2012; Anker et al. 2015; Komai 2015). In this chapter I review the commensals associated with Japanese echiurans based on previous literature and my unpublished data. As a result, it was found that at least 29 species of animals (7 bivalve species, 3 gastropod species, 4 crab species, 7 snapping shrimp species, 1 copepod species, and 7 polychaete species) have been collected from 12 echiuran species.

20.4.1 Commensal Animals of Each Echiuran Species

20.4.1.1 *Urechis unicinctus*

The burrows of *U. unicinctus* are inhabited by three commensal crab species, *Sestrostoma balssi* (Shen, 1932) (Varunidae) (Fig. 20.3h), *Sestrostoma toriumii* Takeda, 1974 (Varunidae), and *Pseudopinnixa carinata* Ortmann, 1894 (Pinnotheridae) (Fig. 20.3g) (Itani et al. 2005), and perhaps by the snapping shrimp *Athanopsis dentipes* Miya, 1980 (Alpheidae) (Miya 1995). In addition, the copepod *Goidelia japonica* Embleton 1901 lives in the rectum (Embleton 1901) and on the body surface of *U. unicinctus* (Anker et al. 2005). The burrows of *U. caupo* of the western coast of North America are used by gobies, clams, crabs, snapping shrimp, and scale worms (MacGinitie and MacGinitie 1968). However, such a diverse commensal community has not been reported from *U. unicinctus* of Japan.

20.4.1.2 *Ikedosoma gogoshimense*

The burrows of *I. gogoshimense* are inhabited by the bivalve *Basterotia gouldi* (A. Adams, 1864) (Basterotiidae, Galeommatoidea) (Fig. 20.3i), *Basterotia recluzi* (A. Adams, 1864) (Basterotiidae, Galeommatoidea), and the snail *Macromphalus tornatilis* (Vanikoridae) (Gould, 1859) (Fig. 20.3n) in the Seto Inland Sea (Goto et al. 2011, 2016a). I have found a scale worm (Lepidonotinae sp. 1) that was collected from burrows of *I. gogoshimense* in mudflats of Hakatajima Island in the Seto Inland Sea (Fig. 20.3t) (Goto, unpublished data).

20.4.1.3 *Ikedosoma elegans*

The snapping shrimp *Alpheus ikedosoma* Komai, 2015 (Alpheidae) was recently described on the basis of materials from Boso Peninsula and Ariake Sea, Japan (Komai 2015). All these specimens were collected from echiuran burrows. The host echiurans from Boso Peninsula were identified as *I. elegans*, whereas those from Ariake Sea were not identified but were probably *I. elegans* or its closely related species (Komai 2015).

20.4.1.4 *Listriolobus sorbillans*

The burrows of *L. sorbillans* are inhabited by the bivalve *Pseudopythina ochetostomae* Morton and Scott 1989 (Kelliidae, Galeommatoidea) (Fig. 20.3m), the crab *Mortensenella forceps* Rathbun, 1909 (Camptandriidae) (Fig. 20.3f), and the snail *Sigaretornus* cf. *planus* (Tornidae) (Fig. 20.3o) (Kosuge et al. 2003; Goto and Kato 2012). In addition, I have found one individual of the bivalve *B.* cf. *borbonica* (Fig. 20.3k) and a scale worm (Polynoinae sp. 1) (Fig. 20.3s) in the burrow of *L. sorbillans* in gravelly sand flats of the northwestern part of Ishigaki Island, Japan (Goto, unpublished data).

20.4.1.5 *Ochetostoma erythrogrammon*

The burrows of *O. erythrogrammon* are inhabited by two snapping shrimp species, *Athanopsis brevirostris* Banner and Banner, 1981 (Alpheidae) (Fig. 20.3b) and *Alpheus barbatus* Coutière, 1897 (Alpheidae) (Fig. 20.3c); one polynoid scale worm, *Lepidonotus* sp. 1 (Fig. 20.3q); three bivalve species, *Basterotia carinata* Goto, Hamamura and Kato 2011, (Fig. 20.3j), *B.* cf. *borbonica* (Fig. 20.3k), and *Byssobornia yamakawai* (Yokoyama, 1922) (Lasaeidae, Galeommatoidea)

(Fig. 20.3l); and one gastropod species (*Phenacolepas* sp. 1, Fig. 20.3p) in the Ryukyu Archipelago, southwestern Japan (Nomura 2000; Goto et al. 2011, 2012; Anker 2012; Goto and Kato 2012; Table 20.3). In addition, unidentified entoprocts were observed on the body surface of commensals (Fig. 20.3w) (Goto, unpublished data). A scale worm (Polynoinae sp. 1) and a black polychaete (Hesionidae sp. 1) (Fig. 20.3r) were found in *O. erythrogrammon* burrows in gravelly sand flats of the northwestern part of Ishigaki Island (Goto, unpublished data). Burrow-associated fauna of *O. erythrogrammon* in the Ryukyu Archipelago differ among populations and are largely categorized into two different types (snapping shrimp-dominant type and scale worm-dominant type), which are probably caused by the difference in bottom sediment characteristics (Goto and Kato 2012). The burrow-associated fauna of *O. erythrogrammon* was also surveyed in Hong Kong (Morton and Morton 1983). However, *O. erythrogrammon* in Morton and Morton (1983) is probably a misidentification of *L. sorbillans* or a closely related species (see Goto and Kato 2012).

20.4.1.6 *Ochetostoma* sp. 1

The snapping shrimp *Alpheus* cf. *barbatus* (Fig. 20.3d) was collected from the burrow of *Ochetostoma* sp. 1 at Chinoura, Kakeromajima, southwestern Japan (Goto, unpublished data).

20.4.1.7 *Ochetostoma* sp. 2

The bivalve *Basterotia* cf. *borbonica* (Fig. 20.3k) and a scale worm (Lepidonotinae sp. 2) (Fig. 20.3u) were collected from burrows of *Ochetostoma* sp. 2 at Edateku, Amami Ōshima, southwestern Japan (Goto, unpublished data).

20.4.1.8 *Ochetostoma* sp.

The snapping shrimp *Alpheus echiurophilus* Anker, Komai, and Marine, 2015 (Alpheidae) was collected from burrows of *Ochetostoma* sp. at Okinawa Island, southwestern Japan (Anker et al. 2015).

20.4.1.9 *Arhynchite hayaoi*

The burrows of *A. hayaoi* are inhabited by the bivalve *B. gouldi* (Fig. 20.3i), *B. recluzi*, and the gastropod *M. tornatilis* (Fig. 20.3n), as observed for *I. gogoshimense* (Goto et al. 2011).

Table 20.3 Symbiotic animals associated with echiurans in Japan

Commensal taxon	Species	Host	Fig. 20.3	References
Bivalvia	*Basterotia carinata* Goto, Hamamura & Kato 2011 (Galeommatoidea)	*Ochetostoma erythrogrammon*	j	Goto et al. (2011) and Goto and Kato (2012)
	Basterotia cf. *borbonica* (Deshayes in Maillard, 1863) (Galeommatoidea)	*Ochetostoma erythrogrammon*, *O. sp. 2*, *Listriolobus sorbillans*	k	Goto and Kato (2012), this study
	Basterotia gouldi (A. Adams, 1864) (Galeommatoidea)	*Ikedosoma gogoshimense*, *Arhynchite hayaoi*	i	Goto et al. (2011)
	Basterotia recluzi (A. Adams, 1864) (Galeommatoidea)	*Ikedosoma gogoshimense*, *Arhynchite hayaoi*	–	Goto et al. (2016a)
	Byssobornia yamakawai (Yokoyama, 1922) (Galeommatoidea)	*Ochetostoma erythrogrammon*	l	Goto and Kato (2012)
	Pseudopythina ochetostomae Morton & Scott, 1989 (Galeommatoidea)	*Listriolobus sorbillans*	m	Morton and Scott (1989) and Kosuge et al. (2003)
	Sagamiscintilla thalassemicola (Habe, 1962) (Galeommatoidea)	*Anelassorhynchus mucosus*	–	Habe (1962)
Gastropoda	*Macromphalus tornatilis* (Gould, 1859) (Vanikoridae)	*Ikedosoma gogoshimense*, *Arhynchite hayaoi*	n	Goto et al. (2011)
	Phenacolepas sp.1 (Phenacolepadidae)	*Ochetostoma erythrogrammon*	p	Goto and Kato (2012)
	Sigaretornus cf. *planus* (A. Adams, 1850) (Tornidae)	*Listriolobus sorbillans*	o	Morton and Morton (1983) and Morton (1988)
Crab	*Mortensenella forceps* Rathubun, 1909 (Camptandriidae)	*Listriolobus sorbillans*	f	Morton and Morton (1983) and Morton (1988)
	Pseudopinnixa carinata Ortmann, 1894 (Pinnotheridae)	*Urechis unicinctus*	g	Itani et al. (2005)
	Sestrostoma balssi (Shen, 1932) (Varunidae)	*Urechis unicinctus*	h	Itani et al. (2005)
	Sestrostoma toriumii (Takeda, 1974) (Varunidae)	*Urechis unicinctus*	–	Itani et al. (2005)

(continued)

Table 20.3 (continued)

Commensal taxon	Species	Host	Fig. 20.3	References
Snapping shrimp	*Alpheus barbatus* Coutière, 1897 (Alpheidae)	*Ochetostoma erythrogrammon*	c	Nomura (2000) and Goto and Kato (2012)
	Alpheus cf. *barbatus* Coutière, 1897 (Alpheidae)	*Ochetostoma* sp. 1	d	This study
	Alpheus echiurophilus Anker et al., 2015 (Alpheidae)	*Ochetostoma* sp.	–	Anker et al. (2015)
	Alpheus ikedosoma Komai, 2015 (Alpheidae)	*Ikedosoma elegans*	–	Komai (2015)
	Athanopsis brevirostris Banner & Banner, 1981 (Alpheidae)	*Ochetostoma erythrogrammon*	b	Anker (2012)
	Athanopsis dentipes Miya, 1980 (Alpheidae)	*Urechis unicinctus*	–	Miya (1995)
	Athanopsis gotoi Anker, 2012 (Alpheidae)	*Anelassorhynchus* sp. 2	a	Anker (2012)
Copeopoda	*Goidelia japonica* Embleton, 1901 (Echiurophilidae)	*Urechis unicinctus*	–	Embleton (1901) and Anker et al. (2005)
Polychaeta	Hesionidae sp. 1	*Ochetostoma erythrogrammon*	r	This study
	Lepidonotus sp. 1 (Polynoidae)	*Ochetostoma erythrogrammon*	q	Goto et al. (2011) and Goto and Kato (2012)
	Lepidonotinae sp. 1 (Polynoidae)	*Ikedosoma gogoshimense*	t	This study
	Lepidonotinae sp. 2 (Polynoidae)	*Ochetostoma* sp. 2	u	This study
	Polynoinae sp. 1 (Polynoidae)	*Listriolobus sorbillans*	s	This study
	Polynoinae sp. 2 (Polynoidae)	*Ochetostoma erythrogrammon*	–	This study
	Polynoidae sp. 1	*Bonellia minor*	v	This study
Entoprocta	unidentified	Various thalassematids	w, x	This study

20.4.1.10 *Bonellia minor*

An unidentified polynoid scale worm was collected from the burrow of *B. minor* in a limestone crevice in southern Okinawa Island (Goto, unpublished data) (Fig. 20.3v). This scale worm is attached to the body surface of *B. minor* (Fig. 20.3v).

20.4.1.11 *Anelassorhynchus mucosus*

The bivalve *Sagamiscintilla thalassemacola* (Habe, 1962) (Galeommatidae, Galeommatoidea) was collected from the body surface of *A. mucosus* (Habe 1962) in Kumamoto, western Japan, although it has not been collected since the first description. The reliability of the host identification in Habe (1962) is not robust.

20.4.1.12 *Anelassorhynchus* sp. 2

The snapping shrimp *Athanopsis gotoi* Anker 2012 (Alpheidae) (Fig. 20.3a) was collected from the burrows of *Anelassorhynchus* sp. 2 (Anker 2012). This shrimp actively moved upon the body surface of the host echiuran (Fig. 20.2f).

20.4.2 Each Commensal Animal Group

20.4.2.1 Bivalvia

All seven echiuran-associated bivalve species in Japan belong to the superfamily Galeommatoidea (Heterodonta) (Table 20.3). This superfamily includes many commensal species that live in burrows of other marine invertebrates (Goto et al. 2012). A symbiotic association with echiurans evolved twice in different lineages of this bivalve group: *Basterotia* and *Pseudopythina*/*Byssobornia* (Goto et al. 2012). Host specificity differs between these groups. *Basterotia* species have been collected from burrows of various thalassematid echiurans (*Ochetostoma*, *Listriolobus*, *Arhynchite*, and *Ikedosoma*; Table 20.3) and each *Basterotia* species also has the ability to use various thalassematids as a host (Table 20.3). On the other hand, *P. ochetostomae* and *B. yamakawai* have only been found in burrows of *L. sorbillans* and *O. erythrogrammon*, respectively. Thus, host specificity is likely more strict in *Pseudopythina*/*Basterotia* species than in *Basterotia* species. Burrow utilization modes also differ between lineages: *Basterotia* live embedded in the burrow wall, whereas *Pseudopythina* and *Byssobornia* live attached to the burrow wall surface (Goto et al. 2011, 2016a; Goto and Kato 2012).

20.4.2.2 Gastropoda

Three gastropod species have been collected from echiuran burrows in Japan (Table 20.3). These gastropods live attached to the burrow wall. *Sigaretornus* cf. *planus* and *Macromphalus tornatilis* are known from the burrows of *L. sorbillans* and *I. gogoshimense*/*Arhynchite hayaoi*, respectively (Goto et al. 2011; Goto and Kato 2012). *Sigaretornus* cf. *planus* was also collected from the burrows of *O. erythrogrammon* in Hong Kong (Morton 1988). However, this is probably a misidentification of *L. sorbillans* (see Goto and Kato 2012). These two gastropods probably have a high specificity to echiuran burrows. On the other hand, the presence of *Phenacolepas* sp. in *O. erythrogrammon* burrows may be accidental, considering that many species of *Phenacolepas* prefer reductive environments under rocks that are embedded in intertidal flats.

20.4.2.3 Alpheidae (Snapping Shrimp)

Ochetostoma species are often utilized by *Alpheus* snapping shrimp as hosts (Nomura 2000; Anker et al. 2007, 2015). Three species of *Alpheus* have been recorded from *Ochetostoma* burrows in Japan (Table 20.3). *Alpheus barbatus* is a dominant commensal of *O. erythrogrammon* in the Ryukyu Archipelago (Nomura 2000; Goto et al. 2011; Goto and Kato 2012). This species is always found under the trunk of the host; it is solitary and sometimes attacks other commensals to exclude them from burrows (Goto and Kato 2012; Goto, unpublished data). This shrimp is unique in having an ability to change body color (Nomura 2000). Some individuals of *A. barbatus* are parasitized by an unidentified isopod (Fig. 20.3e). *Anelassorhynchus* is utilized by *Athanopsis gotoi* as a host. This species actively moves upon the body surface of the host (Fig. 20.2f). In addition, a new *Alpheus* species was recently described from *Ikedosoma* echiuran burrows (Komai 2015). Differing from *A. barbatus*, pairs of male and female were collected from the same echiuran burrows (Komai 2015).

20.4.2.4 Brachyura (Crabs)

Four crab species in three genera and three families have been reported as commensals of echiurans in Japan (Itani et al. 2005). These crabs are also known from burrows of other invertebrates, such as *Upogebia* mud shrimps and sipunculids (Itani et al. 2005; Kosuge 2009). Thus, their host specificity to echiurans is relatively low.

20.4.2.5 'Polychaeta'

Seven polychaete species (mainly scale worms) have been collected from echiuran burrows in Japan (Fig. 20.3q–v; Table 20.3). However, most of them remain unidentified, and their associations with echiurans are mostly unknown. At least one species of *Lepidonotus* (Fig. 20.3q) has high host specificity to *O. erythrogrammon* (Goto and Kato 2012). This species is always solitary (Goto and Kato 2012).

20.4.2.6 Copepoda

One copepod species, *Goidelia japonica*, is known from the rectum and body surface of *U. unicinctus* (Embleton 1901; Anker et al. 2005). Considering that another copepod species, *G. pelliviva*, was recorded from the body surface of thalassematids in Korea (Kim 2000), commensal copepod species may also be associated with thalassematids in Japan.

20.4.2.7 Entoprocta

Entoprocts are often found from thalassematid echiuran burrows and the body surface of other commensal animals in Japan (Fig. 20.3w, x; Goto, unpublished data). At least, they are common in the burrows of *O. erythrogrammon*, *A. hayaoi*, *I. gogoshimense*, and *L. sorbillans* (Goto, unpublished data). Entoprocts were especially dense on the shell surface of the commensal bivalves *B. gouldi* (Fig. 20.3x) and *P. ochetostomae*. However, they remain unidentified, and their associations with host echiurans and other commensals are unknown. In southern Brazil, two entoproct species (*Loxosomella zima* and *L. ditadii*) are known as obligate commensals of the thalassematid echiuran *Lissomyema exilii* (see review in Anker et al. 2005). Thus, the entoprocts found in Japanese echiuran burrows may also be obligate commensals.

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References

Abe H, Sato-Okoshi W, Tanaka M, Okoshi K, Teramoto W, Kondoh T, Nishitani G, Endo Y (2014) Swimming behavior of the spoon worm *Urechis unicinctus* (Annelida: Echiura). Zoology 117:216–223

Anker A (2012) Notes on the Indo-West Pacific shrimp genus *Athanopsis* Coutière, 1897 (Crustacea, Decapoda, Alpheidae), with the description of a new species associated with echiurans (Annelida, Thalassematidae). Zootaxa 3307:48–61

Anker A, Murina GV, Lira C, Vera Caripe JA, Palmer AR, Jeng MS (2005) Macrofauna associated with echiuran burrows: a review with new observations of the innkeeper worm, *Ochetostoma erythrogrammon* Leuckart and Rüppel, in Venezuela. Zool Stud 44:157–190

Anker A, Hurt C, Knowlton N (2007) Three transisthmian snapping shrimps (Crustacea: Decapoda: Alpheidae: *Alpheus*) associated with innkeeper worms (Echiura: Thalassematidae). Zootaxa 1626:1–23

Anker A, Komai T, Marin IN (2015) A new echiuran-associated snapping shrimp (Crustacea: Decapoda: Alpheidae) from the Indo-West Pacific. Zootaxa 3914:441–455

Biseswar R (1997) A new record of the echiuran *Echiurus echiurus* (Pallas, 1767) from the east coast of southern Africa. S Afr J Mar Sci 18:305–308

Biseswar R (2009) The geographic distribution of echiurans in the Atlantic Ocean (phylum Echiura). Zootaxa 2222:17–30

Biseswar R (2010) Zoogeography of the echiuran fauna of the Indo-West Pacific Ocean (Phylum: Echiura). Zootaxa 2727:21–33

Biseswar R (2012) Zoogeography of the echiuran fauna of the East Pacific Ocean (phylum: Echiura). Zootaxa 3479:69–76

Bock S (1942) On the structure and affinities of "*Thalassema*" *lankesteri* Herdman and the classification of the group Echiuroidea. Göteborgs Kungl Vetensk Samhälles Handl Ser B 2:1–94

Chuang SH (1962) Feeding mechanism of the echiuroid, *Ochetostoma erythrogrammon* Leuckart & Rueppell, 1828. Biol Bull 123:80–85

DattaGupta AK (1976) Classification above the generic level in echiurans. In: Rice ME, Todorovic M (eds) Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura, vol 2. Naucno Delo Press, Belgrade, pp 111–118

DattaGupta AK, Menon PKB (1976) The status of the species *Ikedosoma pirotansis* Menon and DattaGupta and a possible rearrangement of the genera under families. In: Rice ME, Todorovic M (eds) Proceedings of the international symposium on the biology of the Sipuncula and Echiura, vol 2. Naucno Delo Press, Belgrade, pp 135–141

Ditadi ASF (1982) On the burrows of echiuran worms (Echiura): a survey. Bol Zool Univ São Paulo 7:21–36

Edmonds SJ (2000) The phylum Echiura. In: Beesley PL, Ross GJB, Glasby CJ (eds) Polychaetes & allies: the southern synthesis. CSIRO Publishing, Melbourne, pp 353–374

Embleton AL (1901) *Goidelia japonica*—a new entozoic copepod from Japan, associated with an infusorian (Trichodina). J Linn Soc Lond Zool 28:211–229

Fisher WK (1946) Echiuroid worms of the North Pacific Ocean. Proc US Natl Mus 96:215–292

Fisher WK (1948) A review of the Bonelliidae. Ann Mag Nat Hist 11:857–860

Fisher WK (1949) Additions to the echiuroid fauna of the North Pacific Ocean. Proc US Natl Mus 99:479–497

Fisher WK, MacGinitie GE (1928) XVII. The natural history of an echiuroid worm. J Nat Hist 1:204–213

Goto R, Kato M (2012) Geographic mosaic of mutually exclusive dominance of obligate commensals in symbiotic communities associated with a burrowing echiuran worm. Mar Biol 159:319–330

Goto R, Hamamura Y, Kato M (2011) Morphological and ecological adaptation of *Basterotia* bivalves (Galeommatoidea: Sportellidae) to symbiotic association with burrowing echiuran worms. Zool Sci 28:225–234

Goto R, Kawakita A, Ishikawa H, Hamamura Y, Kato M (2012) Molecular phylogeny of the bivalve superfamily Galeommatoidea (Heterodonta, Veneroida) reveals dynamic evolution of symbiotic life style and interphylum host switching. BMC Evol Biol 12:172

Goto R, Okamoto T, Ishikawa H, Hamamura Y, Kato M (2013) Molecular phylogeny of echiuran worms (Phylum: Annelida) reveals evolutionary pattern of feeding mode and sexual dimorphism. PLoS ONE 8:e56809

Goto R (2016) A comprehensive molecular phylogeny of spoon worms (Echiura, Annelida): Implications for morphological evolution, the origin of dwarf males, and habitat shifts. Mol Phylogenet Evol 99:247–260

Goto R, Ishikawa H, Hamamura Y (2016a) The enigmatic genus *Paramya* (Myoidea: Myidae): symbiotic association of an East Asian species with spoon worms (Echiura) and its transfer to the family Basterotiidae (Galeommatoidea). J Mar Biol Assoc UK (in press)

Goto R, Sakamoto S, Hayakawa J, Seike K (2016b) Underwater observations of the giant spoon worm *Ikeda taenioides* (Annelida: Echiura: Ikedidae) in a subtidal soft-bottom environment in northeastern Japan, which survived tsunamis of the 2011 off the Pacific Coast of Tohoku Earthquake. J Oceanogr (in press)

Habe T (1962) *Achasmea thalassemicola* sp. nov., a new commensal bivalve found in an echiuroid, *Thalassema mucosum* Ikeda. Venus 22:117–119

Ikeda I (1901) Real nature of the “Umi-sanada” (“Sanada-yumushi”, new Japanese name). Doubutsugaku Zasshi [Zool Mag Jpn] 13:382–392

Ikeda I (1904) The Gephyrea of Japan. J Coll Sci Imp Univ Tokyo 20:1–87

Ikeda I (1905a) Gephyreans collected by Prof. Dean at Manjuyodi, Southern Negros (Philippine Islands). Annot Zool Jpn 5:169–174

Ikeda I (1905b) On Japanese Gephyreans. Zool Mag (Tokyo) 17:269–275

Ikeda I (1907) On three new and remarkable species of echiuroids (*Bonellia miyajimai*, *Thalassema taenioides* and *T. elegans*). J Coll Sci Imp Univ Tokyo 21:1–64

Ikeda I (1908a) Note on a new deep-sea echiuroid *Protobonellia mitsukurii* nov. gen. et sp. Annot Zool Jpn 6:250–265

Ikeda I (1908b) On a new echiuroid (*Hamingia ijimai*) from Sagami Bay. Annot Zool Jpn 7:61–68

Ikeda I (1910) Notes on a deep-sea echiuroid, *Acanthohamingia shiplei* (nov. gen. and sp.), with remarks on the species *Hamingia ijimai* Ikeda. Q J Microsc Sci 56:135–147

Ikeda I (1924) Further notes on the Gephyrea of Japan with descriptions of some new species from the Marshall, Caroline and Palau Islands. Jpn J Zool 1:23–44

Itani G (2008) Symbioses in estuarine burrows. In: Ishibashi N, Nawa Y (eds) Parasitism and symbiosis. Tokai University Press, Tokyo, pp 217–237 (in Japanese)

Itani G, Izichi M, Ueda H (2005) Crab species collected from the burrows of *Urechis unicinctus* in Hiuchi-nada, the central Seto Inland Sea, Japan. Cancer 14:1–4 [in Japanese with English abstract]

Jaccarini V, Schembri PJ (1977) Feeding and particle selection in the echiuran worm *Bonellia viridis* Rolando (Echiura: Bonelliidae). J Exp Mar Biol Ecol 28:163–181

Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. Annu Rev Mar Sci 7:497–520

Kawaguti S (1968) Electron microscopy on blue-green algae in the body wall of an echiuroid, *Ikedosoma gogoshimense*. Biol J Okayama Univ 14:67–74

Kawaguti S (1971) Blue-green algae in echiuroid worms. In: Cheng TC (ed) Aspects of the biology of symbiosis. University Park Press, Baltimore, pp 265–273

Kim IH (2000) Poecilostomatoid copepods from an intertidal mud flat in the Yellow Sea. J Nat Hist 34:367–432

Komai T (2015) A new species of the snapping shrimp genus *Alpheus* (Crustacea: Decapoda: Caridea: Alpheidae) from Japan, associated with the innkeeper worm *Ikedosoma elegans* (Annelida: Echiura: Echiuridae). Zootaxa 4058:101–111

Kosuge T (2009) Ecological notes on *Mortensenella forceps* Rathbun (Crustacea, Brachyura, Camptandriidae) in Ishigakijima Island, Ryukyu Archipelago, southern Japan; special reference to its occurrence in the burrows of invertebrates belonging to multiple phyla. Biol Mag Okinawa 47:3–9

Kosuge T, Kubo H, Nishikawa T (2003) Distribution and ecology of *Pseudopythina ochetostomae* (Mollusca, Bivalvia, Lasaeidae) dwelling in burrows of echiurans in the Ryukyu Islands, southern Japan (in Japanese with English abstract). Biol Mag Okinawa 41:7–13

Kvist S, Siddall ME (2013) Phylogenomics of Annelida revisited: a cladistic approach using genome-wide expressed sequence tag data mining and examining the effects of missing data. Cladistics 29:435–448

Lanchester WF (1905) On the Sipunculids and Echiurids collected during the “Skeat” Expedition to the Malay Peninsula. Proc Zool Soc Lond 75:35–41

Lehrke J (2012) Phylogeny of Echiura (Annelida, Polychaeta) inferred from morphological and molecular data-implications for character evolution. Ph.D, thesis, Mathematisch-Naturwissenschaflichen Fakultät, Rheinischen Friedrich-Wilhelms-Universität Bonn, Germany

MacGinitie GE, MacGinitie N (1968) Natural history of marine animals, 2nd edn. McGraw-Hill, New York

McHugh D (1997) Molecular evidence that echiurans and pogonophorans are derived annelids. Proc Natl Acad Sci USA 94:8006–8009

Miya Y (1995) Alpheidae. In: Nishimura S (ed) Guide to seashore animals of Japan with color pictures and keys, vol 2. Hoikusha, Osaka, pp 314–330

Morton B (1988) Partnerships in the sea: Hong Kong’s marine symbioses. Hong Kong University Press, Hong Kong

Morton B, Morton J (1983) The sea-shore ecology of Hong Kong. Hong Kong University Press, Hong Kong

Morton B, Scott PH (1989) The Hong Kong Leptonacea (Mollusca: Bivalvia) and their hosts, with description of new species. Asian Mar Biol 6:129–160

Newby WW (1940) The embryology of the echiuroid worm *Urechis caupo*. Mem Am Philos Soc 16:1–219

Nishikawa T (1992) The phylum Echiura. In: Nishimura S (ed) Guide to seashore animals of Japan with color pictures and keys, vol 1. Hoikusha, Osaka, pp 306–309

Nishikawa T (2002) Comments on the taxonomic status of *Ikeda taenioides* (Ikeda, 1904) with some amendments in the classification of the phylum Echiura. Zool Sci 19:1175–1190

Nishikawa T (2004) Synonymy of the West-Pacific echiuran *Listriolobus sorbillans* (Echiura: Echiuridae), with taxonomic notes towards a generic revision. Species Divers 9:109–123

Nishikawa T (2007) Yumushi-doubutsu Mon [Phylum Echiura]. In: Ijima A (ed) Dai nana-kai shizen-kankyou hozen kiso-chousa: senkai-iki seitaikei-chousa (higata-chousa) houkokusyo [The 7th national survey on the natural environment: shallow sea survey (tidal flats)]. Biodiversity Center of Japan, Nature Conservation Bureau, Ministry of the Environment, Fujiyoshida, pp 177–181 [in Japanese]

Nishikawa T (2012) Echiura. In: Japanese Association of Benthology (ed) Threatened animals of Japanese tidal flats: Red Data Book of seashore benthos. Tokai University Press, Hadano, pp 237–238 [in Japanese]

Nomura K (2000) Host and colour variation of *Alpheus barbatus* Coutière (Crustacea, Alpheidae) in Japan. Biol Mag Okinawa 38:59–64

Okuda S (1946) The fauna of Akkeshi Bay. XV. Gephyrea. J Fac Sci Hokkaido Imp Univ Ser VI Zool 9:221–224

Ruggiero MA, Gordon DP, Orrell TM, Bailly N, Bourgoin T, Brusca RC, Cavalier-Smith T, Guiry MD, Krik PM (2015) A higher level classification of all living organisms. PLoS ONE 10: e0119248

Ruppert EE, Fox RS, Barnes RD (2004) Invertebrate zoology: a functional evolutionary approach, 7th edn. Brooks/Cole-Thompson, Belmont

Satô H (1931) Report of the biological survey of Mutsu Bay. 20. Echiuroidea. Sci Rep Tohoku Imp Univ 4th Ser Biol 6:171–184

Satô H (1934) On the sipunculids and echiurids of Onomichi Bay, Japan. Zool Mag (Tokyo) 46:245–253 [in Japanese with English abstract]

Satô H (1937a) Echiuroidea, Sipunculoidea and Priapuloidea obtained in northeast Honshû, Japan. Saito Ho-on Kai Mus Res Bull 12:137–176

Satô H (1937b) Raporto pri la Echiuroidea, Sipunculoidea kaj Priapuloidea en la golfo de Onagawa. Bot Zool (Tokyo) 5:1855–1859

Satô H (1939) Studies on the Echiuroidea, Sipunculoidea and Priapuloidea of Japan. Sci Rep Tohoku Imp Univ 4th Ser Biol 14:339–460

Sedgwick A (1898) A student's textbook of zoology. Swan Sonnenschein & Co Ltd, London

Stephen AC, Edmonds SJ (1972) The phyla Sipuncula and Echiura. Trustees of the British Museum (Natural History), London

Struck TH, Schult N, Kusen T, Hickman E, Bleidorn C, McHugh D, Halanych KM (2007) Annelid phylogeny and the status of Sipuncula and Echiura. BMC Evol Biol 7:57

Struck TH, Paul C, Hill N, Hartmann S, Hösel C, Kube M, Lieb B, Meyer A, Tiedemann R, Pursche G, Bleidorn C (2011) Phylogenomic analyses unravel annelid evolution. Nature (Lond) 471:95–98

Tanaka M, Nishikawa T (2013) A new species of the genus *Arhynchite* (Annelida: Echiura) from sandy flats of Japan, previously referred to as *Thalassema owstoni* Ikeda, 1904. ZooKeys 312:13–21

Tanaka M, Kon T, Nishikawa T (2014) Unraveling a 70-year-old taxonomic puzzle: redefining the genus *Ikedosoma* (Annelida: Echiura) on the basis of morphological and molecular analyses. Zool Sci 31:849–861

Weigert A, Helm C, Meyer M, Nickel B, Arendt D, Hausdorf B, Santos SR, Halanych KM, Purschke G, Bleidorn C, Struck TH (2014) Illuminating the base of the annelid tree using transcriptomics. Mol Biol Evol 31:1391–1401

Zenkevitch LA (1957) A new genus and two new species of deep water Echiuroidea of the far eastern seas and of the north-west Pacific. Tr Inst Okeanologii Akad Nauk SSSR 23:291–295

Zenkevitch LA (1958) The deep-sea echiurids of the north-western part of the Pacific Ocean. Tr Inst Okeanologii Akad Nauk SSSR 27:192–203

Zenkevitch LA (1964) New representatives of deep-sea echiurids *Alomasoma belyaevi* Zenkevitch sp. n. and *Choanostoma filatovae* n. sp. in the Pacific. Zool Zh 43:1863–1864

Zenkevitch LA (1966) The systematics and distribution of abyssal and hadal (ultra-abyssal) Echiuroidea. Galathea Rep 8:175–183

Chapter 21
Diversity of Kinorhyncha in Japan and Phylogenetic Relationships of the Phylum

Hiroshi Yamasaki

Abstract Kinorhyncha is a phylum of marine, meiobenthic, segmented, pseudocoelomate animals. To date, about 230 species of kinorhynchs have been reported worldwide, from habitats including coarse to fine sand, mud, and surfaces/interstices of algae or other invertebrates. Although they are broadly distributed, kinorhynchs have been scarcely studied in Japanese waters. Before the twentieth century, there were only six reports of kinorhynchs from Japan, totaling 4 species in 3 genera. Although the known kinorhynch diversity in Japanese waters has increased markedly in the past 15 years to 16 named and at least 17 unnamed species representing 14 genera, this is likely only a small portion of the actual species diversity in this region. Phylogenetic studies of kinorhynchs began only recently. Recent phylogenetic analyses of molecular data, or of combined morphological and molecular data, have revealed discrepancies between the old classification and phylogenetic relationships among higher kinorhynch taxa. On the basis of phylogenies, the kinorhynch classification has been revised to 2 classes, 3 orders, and 11 families. Although the higher-level phylogeny is fairly well resolved, relationships within and among some taxa remain unclear.

Keywords Kinorhyncha • Meiobenthos • Japanese waters • Species • Phylogeny • Classification

21.1 What Are Kinorhynchs and Where Are They Found?

The phylum Kinorhyncha comprises a group of segmented, pseudocoelomate animals. All kinorhynchs described to date are small marine meiobenthic species, up to 1.04 mm long. The kinorhynch body consists of a head, neck, and 11 trunk segments (Fig. 21.1a, b). The head has a protrusible mouth cone at the anterior end

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and an eversible introvert more posteriorly (Fig. 21.1c, d). The mouth cone bears anteriorly a ring of nine outer oral styles and up to three rings of five or ten inner oral styles. The introvert consists of up to seven rings of spinose, concentrically arranged jointed appendages called spinoscalids and trichoscalids. The scalids anchor the head in the sediment when the introvert extends and retracts, facilitating locomotion through the sediment. The neck consists of 6 to 16 cuticular plates called placids, which act as a closing apparatus when the head is retracted (Figs. 21.1b, c, 21.2b). Each trunk segment consists of a closed cuticular ring, or of one tergal and one to three sternal plates (Fig. 21.2a, c). The number of placids and the plate composition of the trunk segments are diagnostic characters at the family or genus level. The most conspicuous features of the trunk segments are the acicular spines (Figs. 21.1a, b, 21.2a, c–e). Most kinorhynch species have a pair of lateral terminal spines on segment 11, and unpaired acicular spines in mid-dorsal to para-dorsal positions and paired ones in dorsolateral to lateroventral positions on several segments. Some species also have tubules, which appear softer and more flexible than the acicular spines (Fig. 21.2a, b, d). Sensory spots, glandular cell outlets, hairs, and nephridial pores are less evident than the spines and tubules (Fig. 21.2b–f), but their shapes and distribution are sometimes important for identification to the species level.

To date, about 230 kinorhynch species have been reported worldwide, from tropical to polar regions, and from intertidal to abyssal depths (Neuhaus 2013; Sørensen 2013). Several species have been reported from brackish waters (Higgins 1977; Horn 1978; Ostmann et al. 2012; Yamasaki and Fujimoto 2014), and 4 species, *Cateria gerlachi* Higgins, 1968, *Cateria styx* Gerlach, 1956, *Cephalorhyncha liticola* Sørensen, 2008, and *Cephalorhyncha nybakkeni* (Higgins, 1986), have been reported from 10 to 90 cm deep in medium to coarse beach sand (Gerlach 1956; Higgins 1968, 1986; Sørensen 2008). The deepest record is from the Atacama Trench (eastern South Pacific Ocean) at depth of 7800 m, but these kinorhynchs were not identified to species (Danovaro et al. 2002). The deepest record for kinorhynchs identified to species are *Pycnophyes abyssorum* Adrianov and Maiorova, 2015, from 5766 m depth in the Kuril–Kamchatka Trench (Adrianov and Maiorova 2015).

Kinorhynchs occur in various habitats, but most often in muddy sediments, where they can be the third most abundant taxon after nematodes and harpacticoid copepods (Jensen 1983; Herman and Dahms 1992; Santos et al. 2009; Grzelak and Kotwicki 2012). Kinorhynchs also inhabit silt, fine sand, coarse shelly sand, or interstices among other sessile marine organisms, including calcareous algae, kelp, sponges, and colonial hydroids (Moore 1973; Higgins 1977, 1986; Bauer-Nebelsick 1996; Sørensen 2006; Yamasaki et al. 2014). The correlation between kinorhynch faunas and habitat has scarcely been investigated, although Sánchez et al. (2012) indicated that some kinorhynchs show a preference for specific sediment types.

To find kinorhynchs, researchers first collect a sediment sample with any of various devices such as a dredge, bottom grab, or core sampler. To extract kinorhynchs from the sediment sample, the “bubbling-and-blot” method is usually used (Higgins 1988; Sørensen and Pardos 2008) (Fig. 21.3), the efficacy of which is

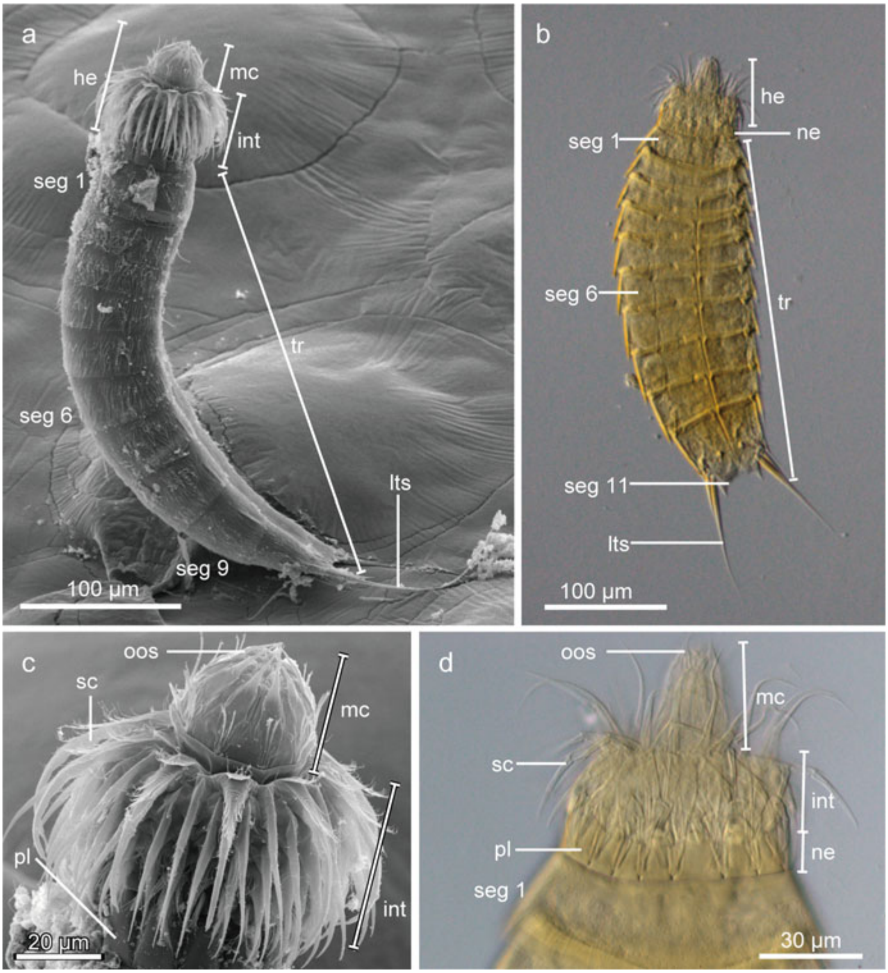

Fig. 21.1 *Echinoderes sensibilis*, scanning electron micrographs (**a**, **c**) and Nomarski differential interference contrast photomicrographs (**b**, **d**). (**a**) Entire body, lateral view. (**b**) Entire body, ventral view. (**c**) Head and neck, lateral view. (**d**) Head, neck, and trunk segment 1, ventral view. *he* head, *int* introvert, *lts* lateral terminal spine, *mc* mouth cone, *ne* neck, *oos* outer oral style, *pl* placid, *sc* scalid, *seg* trunk segment, *tr* trunk

based on the highly hydrophobic kinorhynch cuticle. In this method, a sediment sample and a generous amount of seawater (at least four times the sediment volume) are put into a bucket (Fig. 21.3a, left) and mixed, to break up sediment aggregations (Fig. 21.3a, right). The contents of the bucket are then poured vigorously into an empty bucket, producing many bubbles in the mixture (Fig. 21.3b). Bubbles adhere to kinorhynchs and carry them to the water surface, where they remain suspended by surface tension. The process of pouring from one bucket to the other is repeated several times, after which the sediment settles rapidly, leaving

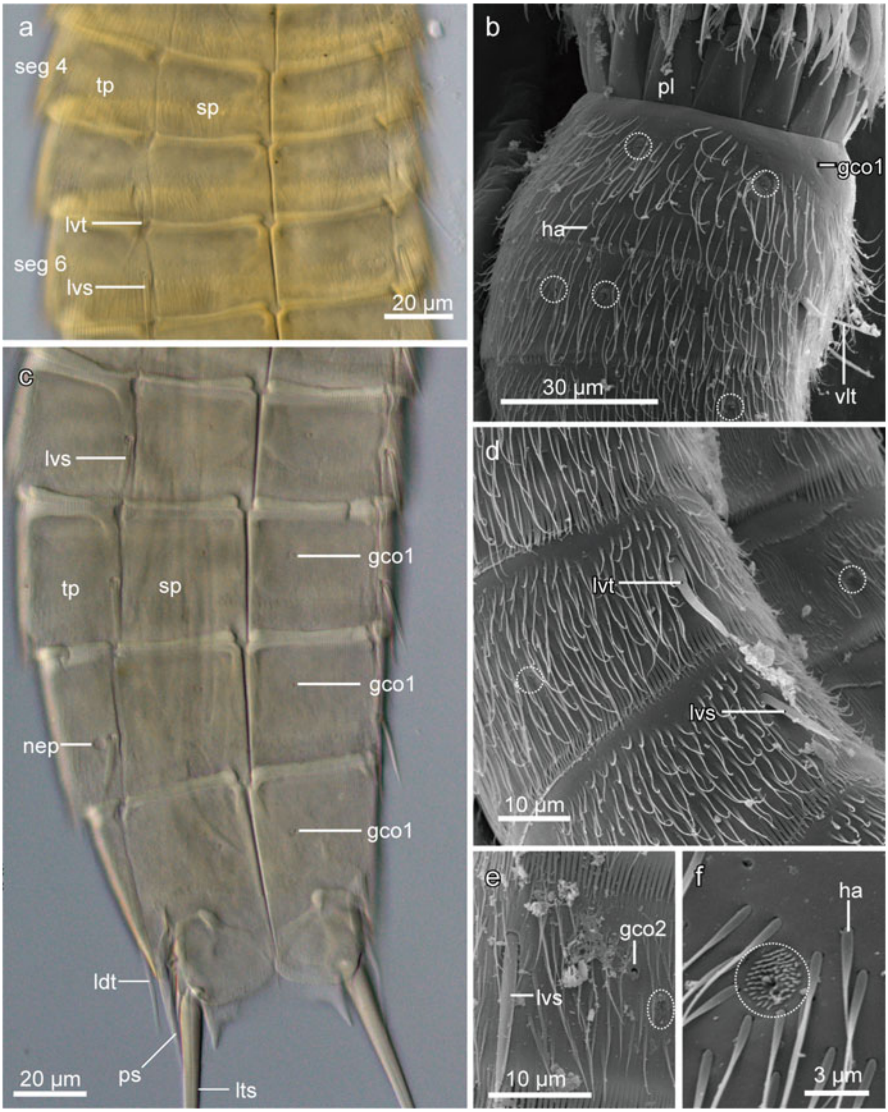

Fig. 21.2 *Echinoderes sensibilis*, Nomarski differential interference contrast photomicrographs (**a**, **c**) and scanning electron micrographs (**b**, **d**–**f**). (**a**) Trunk segments 3–7, ventral view. (**b**) Neck and trunk segments 1–3, lateral view. (**c**) Trunk segments 7–11, ventral view. (**d**) Trunk segments 4–6, lateral view. (**e**) Enlargement of trunk segment 7, ventral view. (**f**) Enlargement of sensory spot on trunk segment 1. *Dashed circles* indicate sensory spots. *gco1* glandular cell outlet type 1, *gco2* glandular cell outlet type 2, *ha* hair, *ldt* laterodorsal tubule, *lts* lateral terminal spine, *lvs* lateroventral acicular spine, *lvt* lateroventral tubule, *nep* nephridial pore, *pl* placid, *ps* penile spine, *seg* trunk segment, *sp* sternal plate, *tp* tergal plate, *vlt* ventrolateral tubule

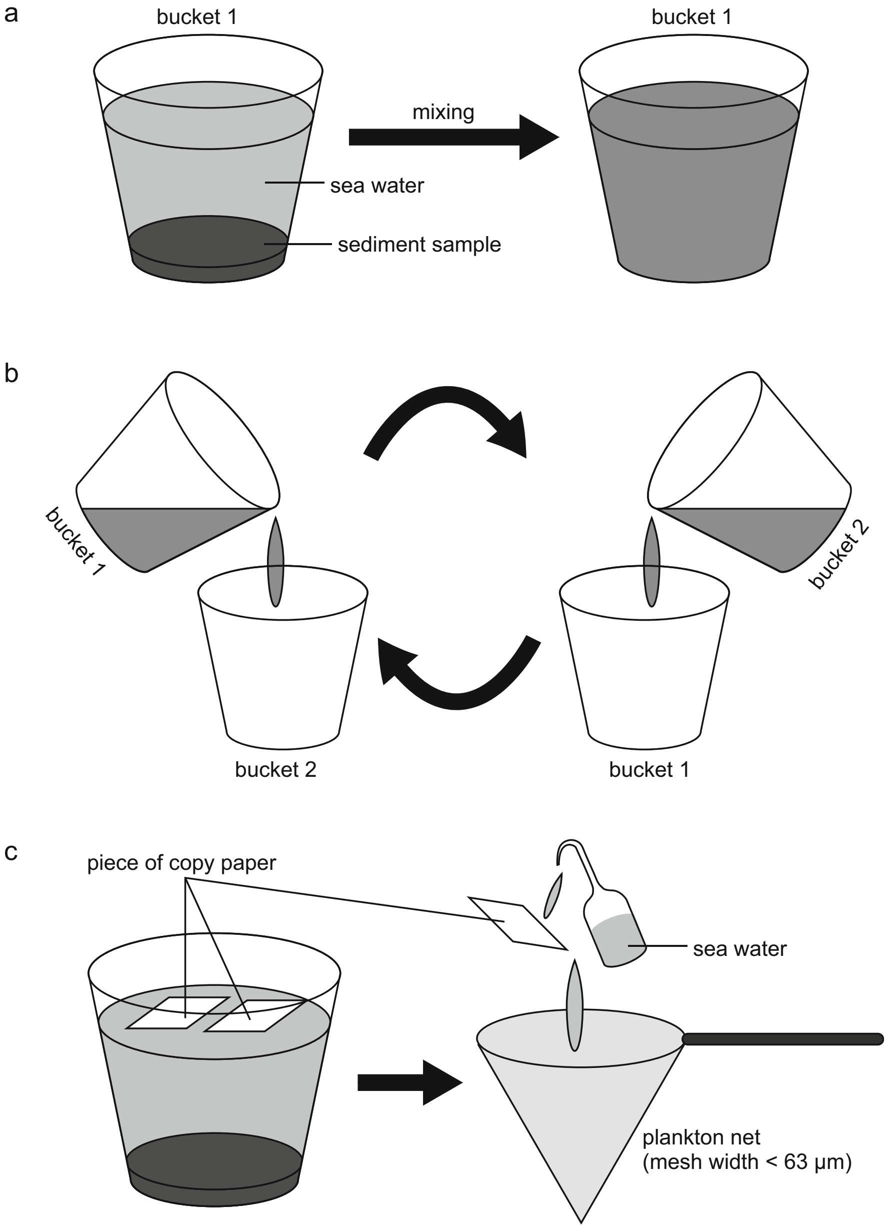

Fig. 21.3 Bubbling-and-blot method. (**a**) Seawater and the sediment sample are put into a bucket and mixed to break sediment aggregations. (**b**) The contents are poured back and forth between buckets several times. (**c**) After the sediment has settled, pieces of copy paper are placed on the surface of the water and picked up, and animals adhering to the paper are washed with seawater into a plankton net

hydrophobic organisms including kinorhynchs floating on the water surface. A piece of copy paper is then gently placed on the surface and pulled up, with the floating organisms attached (Fig. 21.3c left). The attached organisms are then flushed off with seawater into a plankton net with a mesh width less than 63 μm (Fig. 21.3c. right). Material retained in the plankton net is resuspended in seawater in a tray or Petri dish and examined under a stereomicroscope, and kinorhynchs are picked out with an Irwin loop or a pipette. The bubbling-and-blot method is the most effective way to detach most kinorhynchs from the sediment and cuts down the time required in sorting; however, the method does not work well for some intertidal kinorhynch species such as *Echinoderes coulli* Higgins, 1967. To collect such species, use of the centrifugation method (Giere 2009; Neuhaus and Kegel 2015), which is usually used to collect not only kinorhynchs but also other meiofauna, is desirable.

21.2 Research History and Species Diversity of Kinorhyncha in Japan (Table 21.1)

Kinorhynchs were discovered at Saint Malo, northwestern France, by Dujardin (1851), who reported them as “l’Echinodère”. Claparède (1863) described the first species among Dujardin’s “l’Echinodère” as *Echinoderes dujardinii*. A handful of kinorhynch studies were subsequently published in the latter half of the nineteenth century. The earliest kinorhynch specialists were Dr. W. Reinhard who published a paper on kinorhynch morphology, geography, phylogenetic relationships, and description of nine species (Reinhard 1885), and Dr. K. Zelinka, who published a series of papers on kinorhynch taxonomy and the first monograph for the phylum, leading to 46 described species by the first quarter of the twentieth century (Zelinka 1928). Papers by various authors appeared sporadically until the beginning of the 1960s, when Dr. Robert P. Higgins and colleagues made rapid advances in kinorhynch systematics, collecting many kinorhynchs worldwide and describing more than 60 species and 6 new genera. Higgins and his colleagues also contributed to the methodology for studying kinorhynchs; they pioneered the use of the Cobb aluminum slide and the HS slide in kinorhynch study, both of which facilitate detailed observation of the dorsal and ventral sides of single kinorhynchs. Even now, however, relatively few researchers work on kinorhynchs, and study of the group is still in the pioneer stage (Sørensen 2013).

Japanese waters had been one of the least explored regions in the world for kinorhynchs until recently. The first report of a kinorhynch from this region was *Echinoderes masudai* Abe, 1930, from Gogoshima Island in the Seto Inland Sea. The species was found in 1925 by R. Masuda, a student of Dr. Yoshio Abe, during a zoological practicum. Although Abe (1930) described the species as new, it is currently not regarded as valid because of the poor original description (Higgins

Table 21.1 Records of kinorhynchs from Japanese waters

Species	Locality (station in Fig. 21.4)	Habitat	Depth (m)	References
Antygomonas spp.	Amakusa, Kyusyu (24); off Kyusyu Island, East China Sea (25); Ryukyu Islands (33)	–	47–385	Yamasaki et al. (2013)
Campyloderes spp.	Off Amami Island, East China Sea (27); Ryukyu Islands (29)	–	124–1,079	Yamasaki et al. (2013)
Cephalorhyncha asiatica (Adrianov, 1989)	Akkeshi Bay, Hokkaido, Pacific Coast (5)	Muddy sand	13	Yamasaki et al. (2012)
Cephalorhyncha spp.	Hokkaido, Pacific Coast (4, 8)	Mud to muddy sand	15–35	Yamasaki et al. (2013)
Centroderes sp.	Off Amami Island (28)	–	720	Yamasaki (unpubl. data)
Condyloderes setoensis Adrianov et al., 2002b	Tanabe Bay, Honshu, Pacific Coast (17)	Mud	15–27	Adrianov et al. (2002b)
Condyloderes sp.	Sea of Japan (7)	–	1006	Yamasaki et al. (2013)
Dracoderes abei Higgins and Shirayama, 1990	Seto Inalnd Sea (18)	Sandy mud	3	Higgins and Shirayama (1990)
	Seto Inalnd Sea (18, 22, 23); Tanabe Bay, Honshu, Pacific Coast (17)			Sørensen et al. (2012)
Dracoderes snufkini Yamasaki, 2015	Oura Bay, Okinawa Main Island (30); Kabira Bay, Ishigaki Island (34); Iriomote Island (35)	Muddy sand, mud	15–30	Sørensen et al. (2012) and Yamasaki (2015)
Dracoderes toyoshioae Yamasaki, 2015	Off Maeshima (31)	–	697	Yamasaki (2015)
Echinoderidae sp.	Hamatonbetsu, Hokkaido, Okhotsk Sea (1)	Coarse sand	Intertidal	Ito (1985)
Echinoderes aureus Adrianov et al., 2002a	Tanabe Bay, Honshu, Pacific Coast (17)	Brown algae	Intertidal	Adrianov et al. (2002a)
	Bousou Peninsula, Honshu, Pacific Coast (14)	Algae	Intertidal	Murakami (2003)
Echinoderes hwiizaa Yamasaki and Fujimoto, 2014	Ishigaki Island, Ryukyu Islands (34)	Mud	Intertidal flat	Yamasaki and Fujimoto (2014)
Echinoderes komatsui Yamasaki and Fujimoto, 2014	Okinawa Main Island, Ryukyu Islands (30)	Muddy sand	Intertidal flat	Yamasaki and Fujimoto (2014)

(continued)

Table 21.1 (continued)

Species	Locality (station in Fig. 21.4)	Habitat	Depth (m)	References
Echinoderes ohtsukai Yamasaki and Kajihara, 2012	Seto Inland Sea (19)	Muddy sand	Intertidal flat	Yamasaki and Kajihara (2012)
Echinoderes rex Lundbye et al., 2011	Misaki Bay, Honshu, Pacific Coast (15); Tanabe Bay, Honshu, Pacific Coast (17); Seto Inland Sea (21)	Mud to muddy sand	5 to ~30	Yamasaki (unpubl. data)
Echinoderes sensibilis Adrianov et al., 2002c	Tanabe Bay, Honshu, Pacific Coast (17)	Calcareous red algae	Intertidal	Adrianov et al. (2002c)
	Bousou Peninsula, Honshu, Pacific Coast (14)	Algae	Intertidal	Murakami (2003)
	Northern Honshu (11–13), Southern Hokkaido (10)	Algae	Intertidal	Yamasaki et al. (2014)
Echinoderes masudai Abe, 1930 sp. inq.	Gogoshima Island, Seto Inland Sea (20)	–	–	Abe (1930)
Echinoderes cf. *dujardinii*	Ago Bay, Honshu, Pacific Coast (16)	–	–	Tokioka (1949)
	Tanabe Bay, Honshu, Pacific Coast (17)	–	–	Tokioka (1949)
	Kasado Island, Seto Inland Sea (22)	–	–	Sudzuki (1976)
Echinoderes spp.	Hokkaido (3, 5, 6, 9, 10); Northern Honshu (11–13); Seto Inland Sea (22); Ryukyu Islands (32)	–	Intertidal-138	Yamasaki et al. (2013, 2014)
Kinorhynchus yushini Adrianov, 1989	Kasado Island, Seto Inland Sea (22)	–	–	Sudzuki (1976) and Adrianov and Malakhov (1999)
	Oshoro Bay, Hokkaido, Sea of Japan (6)	Muddy sand	8	Yamasaki et al. (2012)
	Seto Inland Sea (19)	Muddy sand	Intertidal flat	Yamasaki and Kajihara (2012)
Kinorhynchus sp.	Oshoro Bay, Hokkaido, Sea of Japan (6)	Sand	25	Ito (1978, 1985)
Meristoderes sp.	Ishigaki Island, Ryukyu Islands (34)	Coarse sand	2	Yamasaki (unpubl. data)
Paracentrophyes anurus Sørensen et al., 2010a	Off Amami Island, East China Sea (28)	–	339	Yamasaki et al. (2013)
Pycnophyes oshoroensis Yamasaki et al., 2012	Oshoro Bay, Hokkaido, Sea of Japan (6)	Muddy sand	8	Yamasaki et al. (2012)

(continued)

Table 21.1 (continued)

Species	Locality (station in Fig. 21.4)	Habitat	Depth (m)	References
Pycnophyes tubuliferus Adrianov, 1989	Tanabe Bay, Honshu, Pacific Coast (17)	Mud	13–25	Murakami et al. (2001)
	Seto Inland Sea (19)	Muddy sand	Intertidal flat	Yamasaki and Kajihara (2012)
Pycnophyes spp.	Northeast Hokkaido (2); Okinawa Main Island, Ryukyu Islands (29)	–	138–204	Yamasaki et al. (2013)
Sphenoderes poseidon Sørensen et al., 2010b	Okinawa Main Island, Ryukyu Islands (29)	–	138	Yamasaki et al. (2013)
Zelinkaderes sp.	Off Tanegashima Island, Kyusyu (26)	–	157	Yamasaki et al. (2013)

1983; Adrianov and Malakhov 1999). Abe (1930) also mentioned an unidentified species of *Echinoderes* that had been found in Misaki Bay on the Pacific side of Honshu a few years before his report. Kawamura (1947) later figured this *Echinoderes* from Misaki Bay in the "Illustrated Encyclopedia of the Fauna of Japan," but no detailed information on the species appeared in either of the publications.

Tokioka (1949) reported the second named kinorhynch species from Japanese waters, collected in 1946 from plankton samples in Ago Bay on the Pacific side of Honshu. He identified his specimens as *E. dujardinii* Claparède, 1863, and similarly reported other *Echinoderes* specimens, collected in 1939 near the Seto Marine Biological Laboratory, as young *E. dujardinii*. These identifications are questionable (Higgins 1983) because they are far from the type locality of this species in Europe.

The first valid, reliably identified species reported from Japan is *Kinorhynchus yushini* Adrianov, 1989, which Sudzuki (1976) had previously reported as *Trachydemus* sp. from Kasado Island in the Seto Inland Sea (*Trachydemus* is now regarded as a junior synonym of *Kinorhynchus*). Adrianov and Malakhov (1999) confirmed that Sudzuki's species is *K. yushini*. Sudzuki (1976) also reported another *Echinoderes* species as *E. dujardinii*, but this likely repeated Tokioka's (1949) misidentification.

Ito (1978) reported kinorhynchs from Oshoro Bay, western Hokkaido, identified initially only as Kinorhyncha sp. but later (Ito 1985) as *Trachydemus* sp. Ito (1985) also reported and illustrated another kinorhynch collected intertidally from a coarse sand beach at Hamatonbetsu, northern Hokkaido, but did not identify it to genus or species; based on the illustration, this species from Hamatonbetsu appears to be an echinoderid.

Higgins and Shirayama (1990) provided the first report from Japan of a new species representing a new genus and family. While collecting near the Mukaishima Marine Biological Station in 1986 to obtain specimens of *E. masudai* for a redescription, these authors found specimens with an unusual number of placids and unique dorsal spines that were alternately displaced laterally, and on the basis of these characters established the new family Dracoderidae, along with the new genus and species *Dracoderes abei* Higgins and Shirayama, 1990. Based on differential interference and phase-contrast microscopy rather than scanning electron microscopy, this original description was somewhat deficient, and Sørensen et al. (2012) redescribed this species in detail.

Three genera and four species (three of them new) were described from Tanabe Bay, central Pacific coast of Honshu Island: *Pycnophyes tubuliferus* Adrianov, 1989; *Echinoderes aureus* Adrianov et al., 2002a; *Echinoderes sensibilis* Adrianov et al., 2002c; and *Condyloderes setoensis* Adrianov et al., 2002b. *Pycnophyes tubuliferus* and *C. setoensis* were found in shallow subtidal sediments (13–27 m depth), whereas *E. aureus* and *E. sensibilis* originated from intertidal brown or calcareous red algae. Murakami (2003) subsequently reported *E. aureus* and *E. sensibilis* from several species of intertidal algae at Kominato, Boso Peninsula, Honshu. Murakami (2005) introduced new standard Japanese names for seven kinorhynchs known from Japanese and adjacent waters.

Since 2012, coworkers and I have described or redescribed eight kinorhynch species from Japan: *Cephalorhyncha asiatica* (Adrianov, 1989) from Akkeshi, eastern Hokkaido; *Kinorhynchus yushini* Adrianov, 1989 and *Pycnophyes oshoroensis* Yamasaki et al., 2012 from Oshoro Bay, western Hokkaido; *Echinoderes ohtsukai* Yamasaki and Kajihara, 2012 from an intertidal flat on the Seto Inland Sea; and *Echinoderes komatsui* Yamasaki and Fujimoto, 2014, *Echinoderes hwiizaa* Yamasaki and Fujimoto, 2014, *Dracoderes snufkini* Yamasaki, 2015, and *Dracoderes toyoshioae* Yamasaki, 2015 from the Ryukyu Islands. I have also collected *Echinoderes rex* Lundbye et al., 2011 from the Seto Inland Sea, Tanabe Bay, and Misaki Bay; and other, undescribed species of *Centroderes*, *Echinoderes*, *Meristoderes*, and *Pycnophyes* from Japanese waters (Yamasaki, unpublished data).

Other studies have focused on the phylogeny and phylogeography of kinorhynchs. Using DNA sequence data, Yamasaki et al. (2013) reconstructed the phylogeny for Japanese kinorhynchs, including *Sphenoderes poseidon* Sørensen et al., 2010a, *Paracentrophyes anurus* Sørensen et al., 2010b, 1 undescribed genus, and 16 possibly undescribed species (3 *Antygomonas*, 2 *Campyloderes*, 1 *Condyloderes*, 2 *Cephalorhyncha*, 5 *Echinoderes*, 1 *Zelinkaderes*, and 2 *Pycnophyes*). Yamasaki et al. (2014) reported a phylogeographic study of two *Echinoderes* species around Hokkaido and northern Honshu.

At the end of the twentieth century, information on kinorhynchs around Japan was fragmentary; there were only six papers dealing with four species (including the non-valid species *E. masudai* and the probably misidentified species *E. dujardini*) representing three genera; this did not mean kinorhynchs were rare around Japan, but only that they had been insufficiently studied. In the past 15 years, knowledge has increased to 16 validly named species and at least

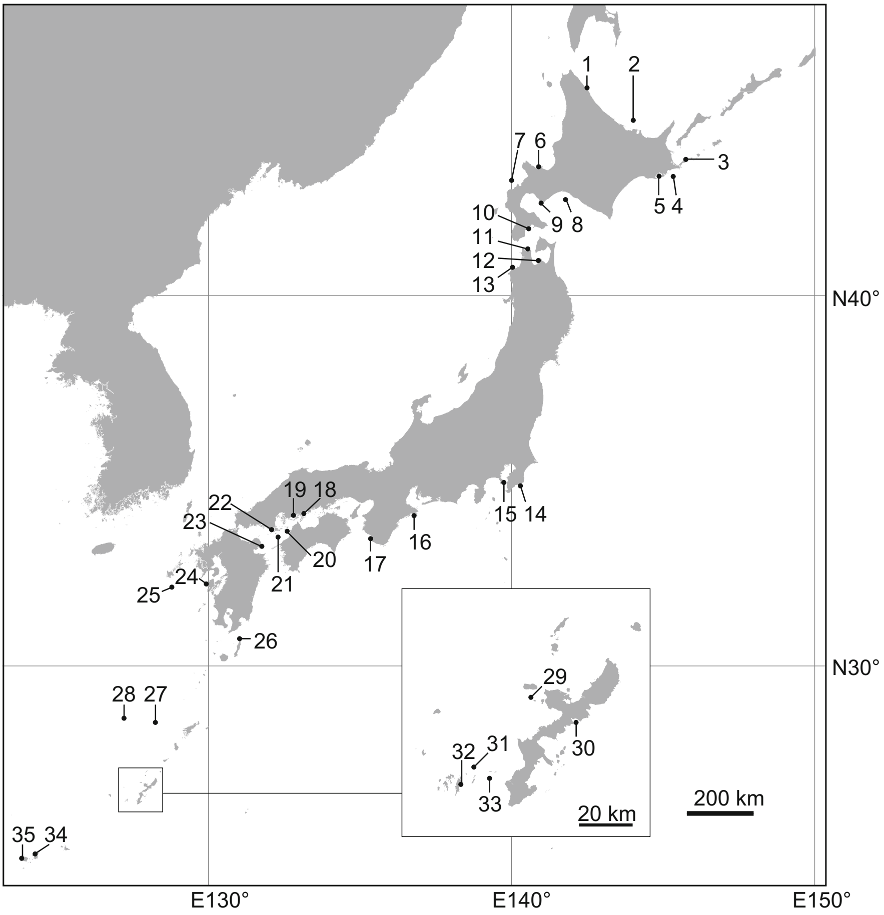

Fig. 21.4 Map showing the stations where kinorhynchs were reported. *Digits* indicate station number. Kinorhynch species reported from each station are listed in Table 21.1

17 unnamed species representing 14 genera (Fig. 21.4, Table 21.1). Nonetheless, this must be only a small proportion of the actual species diversity of kinorhynchs in Japanese waters. I have collected many putatively new species that are awaiting description. Even though kinorhynchs are common and can be easily found and collected around Japan, in many areas no collecting at all has been conducted.

21.3 Relationships of Kinorhyncha with Other Taxa

In the first report about the phylum, Dujardin (1851) believed Kinorhyncha to be phylogenetically situated between crustaceans and worms. Researchers in the twentieth century considered Kinorhyncha to belong to a group of pseudocoelomate animals called Aschelminthes, or Nemathelminthes (Higgins 1988). This group, however, is currently considered to be polyphyletic, and Kinorhyncha is now placed in Ecdysozoa together with Arthropoda, Loricifera, Nematomorpha, Nematoda, Onychophora, Priapulida, and Tardigrada (Zrzavý et al. 1998; Mallatt and Giribet 2006; Sørensen et al. 2008; Hejnol et al. 2009; Dunn et al. 2014; Yamasaki et al. 2015). Within Ecdysozoa, Kinorhyncha is thought to belong to the group Cycloneuralia together with Nematoda, Nematomorpha, Priapulida, and Loricifera, and to comprise the group Scalidophora with the last two phyla. Cycloneuralians have in common an anterior mouth, cylindrical pharynx, and collar-shaped peripharyngeal brain; Scalidophorans have in common rings of scalids on the introvert, flosculi, two rings of longitudinal introvert retractors, compound filter of protonephridia built by more than two terminal cells, and basally thickened cuspidate spines, at least during postembryonic development (Kristensen and Higgins 1991; Nebelsick 1993; Neuhaus 1994; Lemburg 1995; Wallace et al. 1996; Schmidt-Rhaesa et al. 1998; Neuhaus and Higgins 2002; Nielsen 2012; Herranz et al. 2014). Neuhaus (1994) also focused on structures of scalids, spines, pharynx, protonephridia, neck, trunk, flosculi, and urogenital system, proposing three conflicting hypotheses about relationships between Kinorhyncha, Priapulida, and Loricifera: (Kinorhyncha + Priapulida) + Loricifera, Kinorhyncha + (Priapulida + Loricifera), or (Kinorhyncha + Loricifera) + Priapulida (see Neuhaus 1994; Neuhaus and Higgins 2002).

Most molecular phylogenetic studies support the affiliation of Kinorhyncha with Ecdysozoa, as well as the clade comprising Kinorhyncha and Priapulida. These studies also indicate that Kinorhyncha + Priapulida is the most basal ecdysozoan clade (Mallatt and Giribet 2006; Sørensen et al. 2008; Campbell et al. 2011; Rota-Stabelli et al. 2013; Yamasaki et al. 2015). However, molecular phylogenies have generally not supported monophyly for Cycloneuralia or Scalidophora; Cycloneuralia has often appeared as paraphyletic with Nematoda + Nematomorpha being a sister clade of Arthropoda + Onychophora + Tardigrada (Campbell et al. 2011; Pisani et al. 2013; Rota-Stabelli et al. 2013; Yamasaki et al. 2015). Only three molecular studies to date have included representatives for all scalidophoran taxa, and all have rejected the monophyly of Scalidophora, with Loricifera situated in a different clade (Park et al. 2006; Sørensen et al. 2008; Yamasaki et al. 2015).

In summary, although both morphological and molecular data supported Kinorhyncha belonging in Ecdysozoa and closely related to Priapulida, there still has no consensus about the monophyly/paraphyly of Cycloneuralia and Scalidophora..

21.4 Phylogenetic Relationships Within Kinorhyncha, and the Current Classification

Several classifications have been suggested for Kinorhyncha, starting in the early twentieth century. Among these, the system dividing phylum Kinorhyncha into 2 orders, 9 families, and 23 genera (Higgins 1990; Higgins and Shirayama 1990; Adrianov and Malakhov 1994, 1999; Neuhaus and Blasche 2006; Sørensen et al. 2007; Sørensen 2008; Sørensen and Rho 2009; Sørensen and Thormar 2010; Herranz et al. 2012; Dal Zotto et al. 2013; Sánchez et al. 2014) (Table 21.2) has been the most widely accepted, and up to 2015, most taxonomic studies used this system. Only recently have there been attempts to modify the classification to reflect the results of molecular phylogenetic studies.

The first two molecular phylogenetic studies to reconstruct relationships within Kinorhyncha appeared the same year, Yamasaki et al. (2013) using 18S and 28S ribosomal RNA gene sequences from 30 species in 13 genera, and Dal Zotto et al. (2013) using 18S sequences from 48 kinorhynch species in 15 genera, including the morphologically aberrant species *Franciscideres kalenesos* Dal Zotto et al., 2013. Both studies found that neither Cyclorhagida nor Homalorhagida in the old system are monophyletic. Yamasaki et al. (2013) detected four main clades within Kinorhyncha: clade I with Echinoderidae; clade II with Antygomonidae, Semnoderidae, Zelinkaderidae, and two centroderid genera, *Centroderes* and *Condyloderes*; clade III with the centroderid genus *Campyloderes*;

Table 21.2 New classification system of Kinorhyncha proposed in Sørensen et al. (2015), and the multiple entry key to genera

Class	Order	Family	Genus	Characters																		
				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
Allomalorhagida		Dracoderidae	*Dracoderes*	1	2	3	1	-	0	4	-	3	3	2	1	0	1	1	0	1	0	-
		Francisciderida e	*Franciscideres*	1	0	0	1	-	0	1	0	1	1	1	0	0	0	1	0	1	0	-
		Pycnophyidae	*Kinorhynchus*	2	3	1	3	-	0	4	-	3	3	2	0	0	0	0	0	0	0	-
			Pycnophyes	2	3	1	3	-	0	4	-	3	3	2	0	0	0	0	0	1	0	-
		Neocentrophyidae	*Mixtophyes*	2	3	2	2	0	0	4	-	3	3	2	0	0	0	0	0	1	0	-
			Neocentrophyes	2	3	2	2	0	0	4	-	3	3	2	0	0	0	0	0	0	0	-
			Paracentrophyes	2	3	2	2	1	0	4	-	3	3	2	0	0	0	0	0	1	0	-
Cyclorhagida	Echinorhagata	Echinoderidae	*Cephalorhyncha*	1	1	5	1	-	0	3	-	3	3	2	0	0	0	1	0	1	0	-
			Echinoderes	1	1	5	1	-	0	1	0	3	3	2	0	0	0	1	0	1	0	-
			Fissuroderes	1	1	5	1	-	0	4	-	3	3	2	0	0	0	1	0	1	0	-
			Meristoderes	1	1	5	1	-	0	1	1	3	3	2	0	0	0	1	0	1	0	-
			Polacanthoderes	1	1	5	1	-	0	4	-	3	3	2	0	0	0	1	1	1	0	-
	Kentrorhagata	Antygomonidae	*Antygomonas*	1	3	5	1	-	2	4	-	3	3	2	0	1	0	1	0	1	1	1
		Cateriidae	*Cateria*	1	0	0	2	-	0	3	-	2	2	1	0	0	0	1	0	1	1	1
		Centroderidae	*Centroderes*	1	3	5	1	-	0	4	-	3	3	2	0	0	2	1	0	1	1	1
			Condyloderes	1	3	5	1	-	0	4	-	3	3	2	0	1	2	1	0	1	1	2
		Semnoderidae	*Semnoderes*	1	3	5	1	-	1	4	-	3	3	2	0	1	0	1	0	1	1	1
			Sphenoderes	1	3	5	4	-	1	4	-	3	3	2	0	1	0	1	0	1	1	1
		Zelinkaderidae	*Triodontoderes*	1	3	4	1	-	0	4	-	3	1	1	0	1	0	1	0	1	1	1
			Zelinkaderes	1	3	5	1	-	0	1	0	1	1	1	0	1	0	1	0	1	1	1
		incertae sedis	*Tubulideres*	1	3	5	1	-	0	2	-	3	3	2	1	0	0	1	0	1	1	1
		incertae sedis	*Wollunquaderes*	1	3	5	1	-	0	4	-	3	3	2	0	1	2	1	0	1	1	1
	Xenosomata	Campyloderidae	*Campyloderes*	1	3	4	1	-	0	4	-	3	3	2	0	0	2	1	0	1	1	2

and clade IV with Homalorhagida, Dracoderidae, and an undescribed genus. Although these studies pointed out inconsistencies between the old classification and kinorhynch phylogeny, they included representatives of fewer than two thirds of all kinorhynch genera.

Sørensen et al. (2015) addressed the problem of broad taxon sampling by combining morphological with molecular data in a phylogenetic analysis, using morphological data for 60 species in all 23 described genera and 1 undescribed genus, and 18S and 28S sequences for 53 species in 18 genera. The results from this analysis were nearly congruent with those from the two previous studies, at least for relationships among families. Based on their phylogenetic tree, Sørensen et al. (2015) proposed a new classification that divides Kinorhyncha into two classes, Allomalorhagida and Cyclorhagida. Allomalorhagida contains the families Dracoderidae, Franciscideridae, Pycnophyidae, and Neocentrophyidae, and Cyclorhagida is divided into three orders: Echinorhagata (Echinoderidae), Kentrorhagata (Antygomonidae, Cateriidae, Centroderidae, Semnoderidae, Zelinkaderidae), and Xenosomata (Campyloderidae) (Table 21.2).

Although the recent phylogenetic studies have provided the outline of phylogenetic relationships within Kinorhyncha and established a new classification, several problems in kinorhynch phylogeny remain unresolved. The relationship among the cyclorhagid orders remains poorly resolved. In addition, although Echinoderidae contains about half of all kinorhynch species, relationships within the family are poorly resolved, and monophyly needs confirmation for many of the genera. Finally, Kentrorhagata in the new classification (Sørensen et al. 2015) includes 10 of 23 kinorhynch genera, but previous studies have indicated *Antygomonas* is polyphyletic (Dal Zotto et al. 2013; Sørensen et al. 2015) or paraphyletic (Yamasaki et al. 2013), and *Zelinkaderes* is paraphyletic (Dal Zotto et al. 2013). Future morphological and molecular studies using additional taxa and markers will be necessary to resolve these problems.

21.5 Multiple Entry Key to Genera

Table 21.2 shows the new classification system of Kinorhyncha proposed in Sørensen et al. (2015), and the multiple entry key that is modified from table 8 in Neuhaus (2013), with the addition of recently described genera, *Fissuroderes* and *Mixtophyes*, and reduction of characters to simplify the table. Meanings of characters marked with letters (A to S) and digits in the table are explained below.

Habitus	
A	Overall body shape: 1, spindle- to cigar-shaped; 2, box-shaped
Head	
B	Number of trichoscalids (Fig. 21.5a, b): 0, no trichoscalids; 1, 6 trichoscalids; 2, 9 trichoscalids; 3, 14 trichoscalids
Neck	
C	Number of placids (Fig. 21.5a–e): 0, no placids; 1, 6, or 8 placids; 2, 7 placids; 3, 9 placids; 4, 14 placids; 5, 16 placids
Trunk	
D	Plate composition of segment 1 (Fig. 21.5a–f): 1, one ring-like plate; 2, one sternal + one tergal plates; 3, three sternal + one tergal plates; 4, one sternal + one tergal + two lateral plates
E	(When segment 1 consists of one sternal + one tergal plates) subdivision of sternal plate of segment 1: 0, sternal plate without subdivisions; 1, sternal plate partially subdivided into three plates with anterior lines
F	Mid-dorsal and mid-ventral incisions at anterior margin of segment 1: 0, absent; 1, present with forming a clam-shell-like closing apparatus (Fig. 21.5d); 2, present without forming a clam-shell-like closing apparatus (Fig. 21.5e)
G	Plate composition of segment 2 (Fig. 21.5a–f): 1, one ring-like plate; 2, one tergal plate with mid-ventral junction; 3, one sternal + one tergal plates; 4, two sternal + one tergal plates
H	(When segment 2 consists of one ring-like plate) tergosternal divisions in posterior but not anterior part of the segment: 0, absent; 1, present
I	Plate composition of segment segments 3 and 4 (Fig. 21.5a–c, e, f): 1, one tergal plate with mid-ventral junction; 2, one sternal + one tergal plates; 3, two sternal + one tergal plates
J	Plate composition of segment segments 5 and 6: 1, one tergal plate with mid-ventral junction; 2, one sternal + one tergal plates; 3, two sternal + one tergal plates
K	Plate composition of segment segments 7–10 (Fig. 21.5g): 1, one tergal plate with midventral junction; 2, two sternal + one tergal plates
L	Dorsal acicular spines: 0, placed on mid-dorsal line; 1, alternatingly placed to left and right from mid-dorsal line
M	Cuspidate spine (Fig. 21.5e, g): 0, absent; 1, present
N	Lateroventral to ventromedial acicular spines on segment 1 (Fig. 21.5b, f): 0, absent; 1, present in only a few species, and absent in the others; 2, present in all species
O	Acicular lateral spines at least on some of segments 2–9 (Fig. 21.5g, h): 0, absent; 1, present
P	Short acicular spine in ventromedial, ventrolateral, lateral accessory, subdorsal and laterodorsal positions on segments 6 and 7: 0, absent; 1, present
Q	Lateral terminal spine (Fig. 21.5h, i): 0, absent; 1, present
R	Mid-terminal spine (Fig. 21.5h, i): 0, absent; 1, present
S	Length of mid-terminal and lateral terminal spines (Fig. 21.5h, i): 1, mid-terminal spine longer than those of lateral terminal spines; 2, mid-terminal spine shorter than those of lateral terminal spines

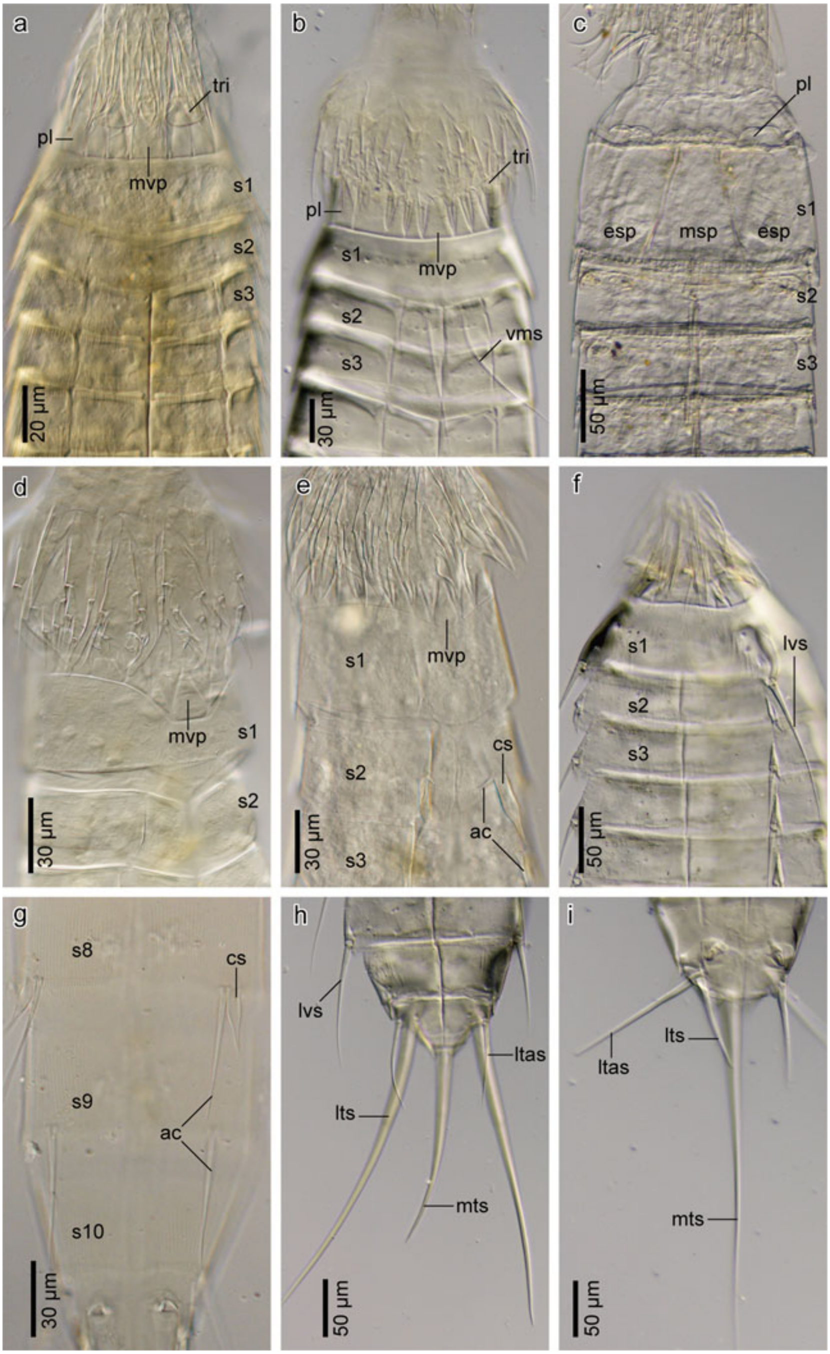

Fig. 21.5 Key characters to identify kinorhynch genus. (**a**) *Echinoderes* sp.: head, neck, and trunk segments 1–5, ventral side. (**b**) *Centroderes* sp.: head, neck, and trunk segments 1–4, ventral side. (**c**) *Pycnophyes* sp.: head, neck, and trunk segments 1–4, ventral side. (**d**) *Sphenoderes poseidon*: head, neck, and trunk segments 1 and 2, lateroventral side. (**e**) *Antygomonas* sp.: head, neck, and

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References

Abe Y (1930) Das Vorkommen von *Echinoderes* in den japanischen Gewässern. J Sci Hiroshima Univ Ser B1(1):39–44

Adrianov AV (1989) First report of kinorhynchs from the Sea of Japan. Zool Zh 61:17–27

Adrianov AV, Maiorova AS (2015) *Pycnophyes abyssorum* sp. n. (Kinorhyncha: Homalorhagida), the deepest kinorhynch species so far. Deep-Sea Res II 111:49–59

Adrianov AV, Malakhov VV (1994) Kinorhyncha: structure, development, phylogeny and taxonomy. Nauka, Moscow [in Russian]

Adrianov AV, Malakhov VV (1999) Kinorhyncha. In: Adrianov AV, Malakhov VV (eds) Cephalorhyncha of the world ocean. KMK Scientific Press, Moscow, pp 82–305

Adrianov AV, Murakami C, Shirayama Y (2002a) *Echinoderes aureus* n. sp. (Kinorhyncha: Cyclorhagida) from Tanabe Bay (Honsyu Island), Japan, with a key to the genus *Echinoderes*. Species Divers 7:47–66

Adrianov AV, Murakami C, Shirayama Y (2002b) Taxonomic study of the Kinorhyncha in Japan. 2. *Condyloderes setoensis*, a new species (Kinorhyncha: Cyclorhagida) from Tanabe Bay (Honshu)—first representative of the genus in the Pacific Ocean. Proc Biol Soc Wash 115:205–216

Adrianov AV, Murakami C, Shirayama Y (2002c) Taxonomic study of the Kinorhyncha in Japan. 3. *Echinoderes sensibilis* n. sp. (Kinorhyncha: Cyclorhagida) from Tanabe Bay. Zool Sci 19:463–473

Bauer-Nebelsick M (1996) *Antygomonas oreas* sp. n., a new deep sea kinorhynch from the Pacific Ocean (Kinorhyncha: Cyclorhagida). Ann Naturhist Mus Wien 98B:5–22

Campbell LI, Rota-Stabelli O, Edgecombe GD, Marchioro T, Longhorn SJ, Telford MJ, Philippe H, Rebecchi L, Peterson KJ, Pisani D (2011) MicroRNAs and phylogenomics resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of Arthropoda. Proc Natl Acad Sci USA 38:15920–15924

Claparède E (1863) Zur Kenntnis der Gattung *Echinoderes* Duj. In: Claparède E (ed) Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie angestellt. Wilhelm Engelmann, Leipzig, pp 90–92, 119, plates XVI–XVII

Fig. 21.5 (continued) trunk segments 1–3, lateroventral side. (**f**) *Campyloderes* cf. *vanhoeffeni*: head, neck, and trunk segments 1–5, ventral side. (**g**) *Zelinkaderes* sp.: trunk segments 8–11, ventral side. (**h**) *Campyloderes* cf. *vanhoeffeni*, trunk segments 9–11, ventral side. (**i**) *Centroderes* sp.: trunk segments 10 and 11, ventral side. *ac* acicular spine, *cs* cuspidate spine, *esp* episternal plate, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral acicular spine, *msp* midsternal plate, *mts* midterminal spine, *mvp* midventral placid, *pl* placid, *s1* trunk segment 1, *s2* trunk segment 2, *s3* trunk segment 3, *s8* trunk segment 8, *s9* trunk segment 9, *s10* trunk segment 10, *tri* trichoscalid plate which is basal plate of trichoscalid, *vms* ventromedial acicular spine

Dal Zotto M, Di Domenico M, Garraffoni A, Sørensen MV (2013) *Franciscideres* gen. nov.—a new, highly aberrant kinorhynch genus from Brazil, with an analysis of its phylogenetic position. Syst Biodivers 11:303–321

Danovaro R, Gambi C, Della Croce N (2002) Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. Deep-Sea Res I 49:843–857

Dujardin F (1851) Sur un petit animal marin, l'Echinodère, formant un type intermédiaire entre les crustacès et les vers. Ann Sci Nat Ser 3 Zool 15:58–173

Dunn CW, Giribet G, Edgecombe GD, Hejnol A (2014) Animal phylogeny and its evolutionary implications. Annu Rev Ecol Evol Syst 45:371–395

Gerlach SA (1956) Üver einen aberranten Vertreter der Kinorhynchen aus dem Küstengrundwasser. Kiel Meeresforsch 12:120–124

Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments. Springer, Berlin

Grzelak K, Kotwicki L (2012) Meiofaunal distribution in Hornsund Fjord, Spitsbergen. Polar Biol 35:269–280

Hejnol A, Obst M, Stamatakis A, Ott M, Rouse GW, Edgecombe GD, Martinez P, Baguñà J, Bailly X, Jondelius U, Wiens M, Müller WEG, Seaver E, Wheeler WC, Martindale MQ, Giribet G, Dunn CW (2009) Assessing the root of bilaterian animals with scalable phylogenetic methods. Proc R Soc B 276:4261–4270

Herman RI, Dahms HU (1992) Meiofauna communities along a depth transect off Halley Bay (Weddell Sea, Antarctica). Polar Biol 12:313–320

Herranz M, Thormar J, Benito J, Sánchez N, Pardos F (2012) *Meristoderes* gen. nov., a new kinorhynch genus, with the description of two new species and their implications for echinoderid phylogeny (Kinorhyncha: Cyclorhagida, Echinoderidae). Zool Anz 251:161–179

Herranz M, Boyle MJ, Pardos F, Neves RC (2014) Comparative myoanatomy of *Echinoderes* (Kinorhyncha): a comprehensive investigation by CLSM and 3D reconstruction. Front Zool 11:31

Higgins RP (1968) Taxonomy and postembryonic development of the Cryptorhagae, a new suborder for the mesopsammic kinorhynch genus *Cateria*. Trans Am Microsc Soc 87:21–39

Higgins RP (1977) Two new species of *Echinoderes* (Kinorhyncha) from South Carolina. Trans Am Microsc Soc 96:340–354

Higgins RP (1983) The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize 2: Kinorhyncha. Smithson Contrib Mar Sci 18:1–131

Higgins RP (1986) A new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from a coarse-sand California beach. Trans Am Microsc Soc 105:266–273

Higgins RP (1988) Kinorhyncha. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC, pp 328–331

Higgins RP (1990) Zelinkaderidae, a new family of cyclorhagid Kinorhyncha. Smithson Contrib Zool 500:1–26

Higgins RP, Shirayama Y (1990) Dracoderidae, a new family of the cyclorhagid Kinorhyncha from the Inland Sea of Japan. Zool Sci 7:939–946

Horn TD (1978) The distribution of *Echinoderes coulli* (Kinorhyncha) along an interstitial salinity gradient. Trans Am Microsc Soc 97:586–589

Ito T (1978) Meiobenthos of a shallow-water sandy bottom in Ishikari Bay, Hokkaido: a general account. J Fac Sci Hokkaido Univ Ser VI 21:287–294

Ito T (1985) Organisms in sand interstices. Kaimeisha, Tokyo [in Japanese]

Jensen P (1983) Meiofaunal abundance and vertical zonation in a sublittoral soft bottom, with a test of the Haps corer. Mar Biol 74:319–326

Kawamura T (1947) Kinorhyncha. In: Uchida S (ed) Illustrated encyclopedia of the fauna of Japan. Hokuryukan, Tokyo, p 1419

Kristensen RM, Higgins RP (1991) Kinorhyncha. In: Harrison FW, Ruppert EE (eds) Microscopic anatomy of invertebrates, vol 4, Aschelminthes. Wiley-Liss, New York, pp 377–404

Lemburg C (1995) Ultrastructure of sense organs and receptor cells of the neck and lorica of the *Halicryptus spinulosus* larva (Priapulida). Microfauna Mar 10:7–30

Lundbye H, Rho HS, Sørensen MV (2011) *Echinoderes rex* n. sp. (Kinorhyncha: Cyclorhagida), the largest *Echinoderes* species found so far. Sci Mar 75:41–51

Mallatt J, Giribet G (2006) Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. Mol Phylogenet Evol 40:772–794

Moore PG (1973) *Campyloderes macquariae* Johnston, 1938 (Kinorhyncha: Cyclorhagida) from the northern hemisphere. J Nat Hist 7:341–354

Murakami C (2003) Study on Kinorhyncha with new record of *Echinoderes aureus* and *Echinoderes sensibilis* from Boso Peninsula, Japan. Annu Rep Mar Biol Res Inst Jpn 43–50 (in Japanese)

Murakami C (2005) A brief review of general biology of Kinorhyncha, with proposed new standard Japanese names for the species from Japan. TAXA (Proc Jpn Soc Syst Zool) 19:34–41 [in Japanese with English abstract]

Murakami C, Adrianov AV, Shirayama Y (2001) Taxonomic study of Kinorhyncha in Japan 1. *Pycnophyes tubuliferus* Adrianov, 1989 (Kinorhyncha: Homalorhagida) from Japan. Publ Seto Mar Biol Lab 39:113–127

Nebelsick M (1993) Introvert, mouth cone, and nervous system of *Echinoderes capitatus* (Kinorhyncha, Cyclorhagida) and implications for the phylogenetic relationships of Kinorhyncha. Zoomorphology 113:211–232

Neuhaus B (1994) Ultrastructure of alimentary canal and body cavity, ground pattern, and phylogenetic relationships of the Kinorhyncha. Microfauna Mar 9:61–156

Neuhaus B (2013) Kinorhyncha (= Echinodera). In: Schmidt-Rhaesa A (ed) Handbook of zoology. Gastrotricha, Cycloneuralia and Gnathifera 1: Nematomorpha, Priapulida, Kinorhyncham, Loricifera. De Gruyter, Berlin, pp 181–348

Neuhaus B, Blasche T (2006) *Fissuroderes*, a new genus of Kinorhyncha (Cyclorhagida) from the deep sea and continental shelf of New Zealand and from the continental shelf of Costa Rica. Zool Anz 245:19–52

Neuhaus B, Higgins RP (2002) Ultrastructure, biology, and phylogenetic relationships of Kinorhyncha. Integr Comp Biol 42:619–632

Neuhaus B, Kegel A (2015) Redescription of *Cateria gerlachi* (Kinorhyncha, Cyclorhagida) from Sri Lanka and of *C. styx* from Brazil, with notes on *C. gerlachi* from India and *C. styx* from Chile, and the ground pattern of the genus. Zootaxa 3965:1–77

Nielsen C (2012) Animal evolution: interrelationships of the living phyla, 3rd edn. Oxford University Press, Oxford

Ostmann A, Nordhaus I, Sørensen MV (2012) First recording of kinorhynchs from Java, with the description of a new brackish water species from a mangrove-fringed lagoon. Mar Biodivers 42:79–91

Park JK, Rho HS, Kristensen RM, Kim W, Giribet G (2006) First molecular data on the phylum Loricifera—an investigation into the phylogeny of Ecdysozoa with emphasis on the positions of Loricifera and Priapulida. Zool Sci 23:943–954

Pisani D, Carton R, Campbell LI, Akanni WA, Mulville E, Rota-Stabelli R (2013) An overview of arthropod genomics, mitogenomics, and the evolutionary origins of the arthropod proteome. In: Minelli A, Boxshall G, Fusco G (eds) Arthropod biology and evolution: molecules, development, morphology. Springer, Heidelberg, pp 41–61

Reinhard W (1885) Kinorhyncha (*Echinoderes*), leur structure anatomique et leur place dans le système. Trav Soc Nat Univ Imp Kharkow 19:205–305

Rota-Stabelli O, Daley AC, Pisani D (2013) Molecular timetrees reveal a Cambrian colonization of land and a new scenario for ecdysozoan evolution. Curr Biol 23:392–398

Sánchez N, Herranz M, Benito J, Pardos F (2012) Kinorhyncha from the Iberian Peninsula: new data from the first intensive sampling campaigns. Zootaxa 3402:24–44

Sánchez N, Pardos F, Sørensen M (2014) A new kinorhynch genus, *Mixtophyes* (Kinorhyncha: Homalorhagida), from the Guinea Basin deep-sea, with new data on the family Neocentrophyidae. Helgol Mar Res 68:221–239

Santos PJP, Botter-Carvalho ML, do Nascimento-Júnior AB, Marinho RGC, Carvalho PVVC, Valença APMC (2009) Response of estuarine meiofuana assemblage to effects of fertilizer enrichment used in the sugar cane monoculture. Pernambuco, Brazil. Braz J Oceanogr 57:43–55

Schmidt-Rhaesa A, Bartolomaeus T, Lemburg C, Ehlers U, Garey JR (1998) The position of the Arthropoda in the phylogenetic system. J Morphol 238:263–285

Sørensen MV (2006) New kinorhynchs from Panama, with a discussion of some phylogenetically significant cuticular structures. Meiofauna Mar 15:51–77

Sørensen MV (2008) A new kinorhynch genus from the Antarctic deep sea and a new species of *Cephalorhyncha* from Hawaii (Kinorhyncha: Cyclorhagida: Echinoderidae). Org Divers Evol 8:230e1–230e18

Sørensen MV (2013) Phylum Kinorhyncha. Zootaxa 3703:63–66

Sørensen MV, Pardos F (2008) Kinorhynch systematics and biology: an introduction to the study of kinorhynchs, inclusive identification keys to the genera. Meiofauna Mar 16:21–73

Sørensen MV, Rho HS (2009) *Triodontoderes annulap* gen. et sp. nov.: a new cyclorhagid kinorhynch genus and species from Micronesia. J Mar Biol Assoc UK 89:1269–1279

Sørensen MV, Thormar J (2010) *Wollunquaderes majkenae* gen. et sp. nov.: a new cyclorhagid kinorhynch genus and species from the Coral Sea, Australia. Mar Biodivers 40:261–275

Sørensen MV, Heiner I, Ziemer O, Neuhaus B (2007) *Tubulideres seminoli* gen. et sp. nov. and *Zelinkaderes brightae* sp. nov. (Kinorhyncha, Cyclorhagida) from Florida. Helgol Mar Res 61:247–265

Sørensen MV, Hebsgaard MB, Heiner I, Glenner H, Willerslev E, Kristensen RM (2008) New data from an enigmatic phylum: evidence from molecular sequence data supports a sister-group relationship between Loricifera and Nematomorpha. J Zool Syst Evol Res 46:231–239

Sørensen MV, Pardos F, Herranz M, Rho HS (2010a) New data on the genus *Paracentrophyes* (Homalorhagida, Kinorhyncha), with the description of a new species from the West Pacific. Open Zool J 3:42–59

Sørensen MV, Rho HS, Kim D (2010b) A new species of the rare genus *Sphenoderes* (Cyclorhagida, Kinorhyncha), with differential notes on *S. indicus* Higgins, 1969. Mar Biol Res 6:472–484

Sørensen MV, Herranz M, Rho HS, Min WG, Yamasaki H, Sánchez N, Pardos F (2012) On the genus *Dracoderes* Higgins & Shirayama, 1990 (Kinorhyncha: Cyclorhagida) with a redescription of its type species, *D. abei*, and a description of new species from Spain. Mar Biol Res 8:210–232

Sørensen MV, Dal Zotto M, Rho HS, Herranz M, Sánchez N, Pardos F, Yamasaki H (2015) Phylogeny of Kinorhyncha based on morphology and two molecular loci. PLoS ONE 10: e0133440

Sudzuki M (1976) Microscopical marine animals scarcely known from Japan, 1: micro- & meiofaunae around Kasado Island in the Seto Inland Sea of Japan. Proc Jap Soc Syst Zool 12:5–12

Tokioka T (1949) Notes on *Echinoderes* found in Japan. Publ Seto Mar Biol Lab 1:67–69

Wallace RL, Ricci C, Melone G (1996) A cladistic analysis of pseudocoelomate (aschelminth) morphology. Invertebr Biol 115:104–112

Yamasaki H (2015) Two new species of *Dracoderes* (Kinorhyncha: Dracoderidae) from the Ryukyu Islands, Japan, with a molecular phylogeny of the genus. Zootaxa 3980:359–378

Yamasaki H, Fujimoto S (2014) Two new species in the *Echinoderes coulli* group (Echinoderidae, Cyclorhagida, Kinorhyncha) from the Ryukyu Islands, Japan. ZooKeys 382:27–52

Yamasaki H, Kajihara H (2012) A new brackish-water species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Seto Inland Sea, Japan. Species Divers 17:109–118

Yamasaki H, Kajihara H, Mawatari SF (2012) First report of kinorhynchs from Hokkaido, Japan, including a new species of *Pycnophyes* (Pycnophyidae: Homalorhagida). Zootaxa 3425:23–41

Yamasaki H, Hiruta SF, Kajihara H (2013) Molecular phylogeny of kinorhynchs. Mol Phylogenet Evol 67:303–310

Yamasaki H, Hiruta SF, Kajihara H, Dick MH (2014) Two kinorhynch species (Cyclorhagida, Echinoderidae, *Echinoderes*) show different distribution patterns across Tsugaru Strait, Northern Japan. Zool Sci 31:421–429

Yamasaki H, Fujimoto S, Miyazaki K (2015) Phylogenetic position of Loricifera inferred from nearly complete 18S and 28S rRNA gene sequences. Zool Lett 1:18

Zelinka K (1928) Monographie der Echinodera. Wilhelm Engelmann, Leipzig

Zrzavý J, Mihulka S, Kepka P, Bezděk A, Tietz D (1998) Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. Cladistics 14:249–285

Chapter 22
Copepod Biodiversity in Japan: Recent Advances in Japanese Copepodology

Susumu Ohtsuka and Shuhei Nishida

Abstract Recent advances in our understanding of the biodiversity of copepods in Japanese waters are briefly reviewed. It is noteworthy that the two new species of Platycopioida found in Japan are the first record of this order from the Indo-Pacific. Taxonomic revisions of calanoids in Japanese waters have continued based on both morphological and molecular data. Molecular analyses have revealed the presence of cryptic/sibling species in a common species and of intraspecific variations. Complete mitochondrial DNA sequences from copepods have been analyzed for *Tigriopus japonicus*, which suggest that copepods are genetically 'eccentric.' Molecular tools have helped to clarify the phylogenetic relationships of highly modified symbiotic copepods. Population dynamics, life cycles, and distributions of planktonic copepods have been thoroughly investigated in coastal and oceanic waters. These studies highlighted the influence of the Oyashio/Kuroshio currents on the coast, the high mortality of eggs from predation, adaptive responses to phytoplankton blooms, and niche partitioning by habitat and food. Deep-sea calanoids are highly diverse and specialized for detritivory and carnivory. East Asian planktonic copepods have been introduced to America and Europe via ballast water, although Japan not yet received any alien planktonic copepods. In contrast, parasitic copepods have been introduced to Japan via aquaculture. The life cycle of commercially important sea lice was clarified. Because copepods are one of the most abundant metazoans on Earth, more biological but also biomimetic information should be accumulated.

Keywords Alien • Copepod • Indo-West Pacific • Partition • Relict • Zoogeography

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22.1 Introduction

The subclass Copepoda currently includes about 13,000 species of small planktonic, benthic, and symbiotic crustaceans (Huys and Boxshall 1991; Boxshall and Halsey 2004; Boxshall and Defaye 2008). However, this species richness represents a fraction of the real diversity because of the low taxonomic resolution, especially in symbiotic taxa. For example, only 1.3 % of invertebrates and 16.0 % of fish have been reported to harbor symbiotic copepods (Ho 2001). Deep-sea hyperbenthic copepods require specially designed gear such as baited traps and plankton nets fished from deep-sea vessels (e.g., Grice and Hulsemann 1970; Fleminger 1983; Nishida et al. 1999; Bradford-Grieve 2002, 2004; Ivanenko et al. 2007; Markhaseva and Schulz 2008). Because small-sized crustaceans are not directly related to human society as commodities, taxonomic information is largely restricted to two groups: planktonic copepods that are main prey items of commercially important fish, and parasitic copepods which are pests in aquaculture.

Free-living copepods are a key link between primary producers and higher tropic levels in aquatic ecosystems and are considered to be one of the most numerous organisms on Earth (Huys and Boxshall 1991). Taxonomic and ecological research has been focused mainly on planktonic copepods since the first scientific description of a copepod, *Calanus finmarchicus*, by Johan Gunnerus in 1770. Parasitic copepods, such as sea lice (Caligidae and related taxa), have caused serious economic losses in aquaculture, estimated at more than 100 million US$ (Ho and Lin 2004). More attention is being paid to sea lice and other parasites consequent to the expansion of aquaculture.

In Japan, Mr. Takamochi Mori (1902–1945) and Dr. Otohiko Tanaka (1902–1990), and Dr. Tatsunori Itô (1945–1990) made great contributions to the taxonomic knowledge of marine planktonic and benthic copepods, respectively (Kikuchi 1991; Omori 2002; Ohtsuka et al. 2015). Drs. Satyu Yamaguchi (1894–1976) and Sueo Shiino (1908–1978) provided the taxonomic benchmarks for symbiotic copepods (Ooishi 1979). Succeeding generations of Japanese copepodologists have built on these pioneering studies.

Since the Showa Era, marine zooplanktology in Japan, including copepodology, has been at the forefront of global research, mainly because of the excellence of the plankton laboratories in Hokkaido University and the University of Tokyo (Omori 2002). Japanese copepodologists have specialized in robust taxonomic and functional morphological work; extensive ecological studies on the distribution, life cycle, and population dynamics; and detailed molecular analyses. In contrast, Japanese parasitology involved with symbiotic copepods has been impacted by the lack of an integrated educational system.

New and amazing discoveries concerning the taxonomy, phylogeny, evolution, zoogeography, and ecology of free-living and parasitic copepods have been made by Japanese copepodologists, contributing much to our understanding of biodiversity, some of which are summarized herein. Mauchline (1998) published a comprehensive monograph on the biology of calanoid copepods; therefore, our focus is on subsequent studies on free-living copepods and the recent advances in research on symbiotic taxa.

22.2 Taxonomy

22.2.1 Order Platycopioida: Importance of Near-Bottom and Cave Faunas

The order Platycopioida comprises the infraclass Progymnoplea established by Huys and Boxshall (1991) and retains primitive features in comparison with other orders. Its distribution is restricted to hyperbenthic layers and caves (Fosshagen and Iliffee 1985, 1988; Arbizu 1997; Boxshall and Halsey 2004). Two species of platycopioids occur in shallow near-bottom waters off the Nansei Islands, southern Japan, and are the only records of the order in the Indo-Pacific: *Platycopia orientalis* and *P. compacta* (Fig. 22.1a) (Ohtsuka and Boxshall 1994; Ohtsuka et al. 1998). Based on their circumglobal distribution, Ohtsuka et al. (1998) suggested that platycopioids exhibit a Tethyan track.

No cavernicolous platycopioids are known from Japan, but there are many marine limestone caves in the Ryukyu Islands (Kase and Hayami 1992), so cavernicolous taxa such as *Antrisocopia* and *Nanocopia* (Fosshagen and Iliffee, 1985, 1988) might be found there. The highly specialized cave-living crustacean class Remipedia is restricted to the East and West Atlantic and South Pacific (Yager and Humphreys 1996; Neibar et al. 2011). Our present awareness of cave-living crustaceans in the North Pacific is low. The discovery of a new thermosbaenacean from an anchialine cave in the Nansei Islands (Shimomura and Fujita 2009) suggests that a comprehensive survey of marine cave-living animals in Japan is necessary.

22.2.2 Order Calanoida: Revisions of Common Species and Discovery of New Hyperbenthic Taxa

The taxonomy of brackish and coastal calanoids, the best-studied group in Japanese copepodology, has been revised by integrative molecular and morphological analyses. Such studies revealed the presence of many cryptic or sibling species among common species; for example, *Acartia pacifica* is a common, warm-water species on the coast of Japan, but a closely related species *A. ohtsukai* was recognized from the Ariake Sea and is regarded as a continental relict (Ueda and Bucklin 2006; Sakaguchi et al. 2011). *Pseudodiaptomus inopinus* dominates brackish waters of Japan, but its populations in the Nansei Islands, southernmost Japan, proved to represent a distinct sibling species, *P. nansei* (Sakaguchi and Ueda, 2010). Recently, new species of abundant genera were found: *Centropages maigo* from

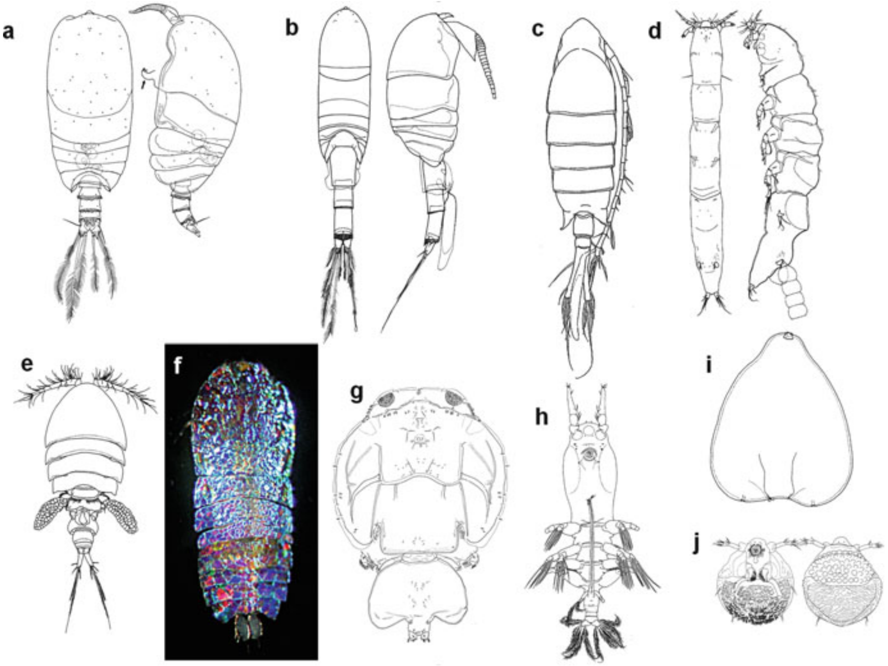

Fig. 22.1 Copepods newly described or previously recorded from Japan. (**a**) Basal copepod *Platycopia compacta*, female, dorsal (*left*) and lateral view, ventral hook *arrowed* (body length = ~0.8 mm). (**b**) Near-bottom calanoid *Placocalanus inermis*, female, dorsal (*left*) and lateral (*right*) view (0.45 mm). (**c**) Calanoid *Tortanus* (*Eutortanus*) *komachi* endemic to Japan, female, dorsal view (~3.0 mm). (**d**) Poecilostomatoid *Umazuracola elongatus* parasitic on skins of black scraper, female, dorsal (*left*) and lateral (*right*) view (~1.0 mm). (**e**) "Poecilostomatoid" *Hemicyclops gomsoensis*, female, dorsal view (~1.6 mm). (**f**) "Poecilostomatoid" *Sapphirina metallina*, male, dorsal view (~2.1 mm). (**g**) Siphonostomatoid *Caligus sclerotinosus*, female, dorsal view (~3.0 mm). (**h**) Monstrilloid *Maemonstrilla turgida*, female, ventral view (~1.6 mm). **i** Siphonostomatoid *Neomysidion rahotsu*, female, dorsal view (~0.8 mm). (**j**) *Neomysidion rahotsu*, dwarf male, ventral (*left*) and dorsal (*right*) view (~0.1 mm) (After: (**a**) Ohtsuka et al. 1998; (**b**) Ohtsuka et al. 1996b; (**c**) Itoh et al. 2001; (**d**) Ho et al. 2006; (**e**) Itoh and Nishida 2007; (**f**) original, through the courtesy of Prof. Jun Nishikawa; (**g**) Ho et al. 2004; (**h**) Grygier and Ohtsuka 2008;(**i**, **j**) Ohtsuka et al. 2005a; with permission from the Zoological Society of Japan (**a**, **d**), Taylor & Francis (**b**), the Plankton Society of Japan (**c**, **e**), Springer-Verlag (**g**, **i**, **j**), and John Wiley (**h**))

Hokkaido, Honshu, and Shikoku Islands (Ohtsuka et al. 2005c); *Labidocera churaumi* from Okinawa (Hirabayashi and Ohtsuka 2014); and *Tortanus komachi* (Fig. 22.1c) from the coast of the Japan Sea (Itoh et al. 2001).

The taxonomy of the Paracalanidae has been confused at family, generic, and species levels (Hiromi 1981, 1987; Boxshall and Halsey 2004; Cornils and Blanco-Bercial 2013). The Calocalanidae and Mecynoceridae are synonymous with the Paracalanidae on the basis of morphological and molecular data, although two of these families were previously separated (Boxshall and Halsey 2004; Cornils and Blanco-Bercial 2013). According to the molecular analysis by Cornils and

Table 22.1 Common planktonic copepods in the brackish and coastal waters of Japan

Location	Common species	References
Akkeshi Bay, Lake Akkeshi	*Acartia hudsonica*, *A. longiremis*, *Centropages abdominalis*, *Eurytemora herdmani*, *E. pacifica*, *Paracalanus parvus* s.l., *Pseudocalanus newmani*, *Oithona similis**	Ueda (2001)
Ishikari Bay, Hokkaido	*Clausocalanus pergens*, *Mesocalanus tenuicornis*, *Metridia pacifica*, *Neocalanus flemingeri*, *N. plumcrus*, *Pseudocalanus newmani*, *Oithona* spp.*	Asami et al. (2010)
Funka Bay, Hokkaido	*Acartia* spp., *Calanus pacificus*, *Clausocalanus* spp., *Paracalanus* sp., *Metridia pacifica*, *Pseudocalanus newmani*	Ban et al. (1998)
Onagawa Bay, Honshu	*Acartia omorii* (as *A. clausi*), *Calanus pacificus*, *Eurytemora pacifica*, *Paracalanus parvus* s.l., *Pseudocalanus minutus*, *Oithona similis**	Uye (1982)
Okkirai Bay, Honshu	*Acartia hudsonica*, *A. longiremis*, *A. omorii*, *A. steueri* (*Acartia* only)	Yamada et al. (2012)
Toyama Bay, Honshu	*Ctenocalanus vanus*, *Mesocalanus tenuicornis*, *Metridia pacifica*, *Paracalanus* sp., *Paraeuchaeta elongata* (as *E. japonica*), *Pseudocalanus minutus*, *Scolecithricella dentata*, *Oithona atlantica**	Hirakawa et al. (1992)
Tokyo Bay	*Acartia omorii*, *A. sinjiensis*, *Calanus sinicus*, *Labidocera rotunda*, *Paracalanus parvus* s.l., *Pseudodiaptomus marinus*, *Oithona davisae**, *Hemicyclops japonicus***	Itoh et al. (2011)
Maizuru Bay, Honshu	*Acartia erythraea*, *A. hudsonica*, *A. omorii*, *A. sinjiensis*, *Centropages abdominalis*, *Paracalanus parvus* s.l., *Parvocalanus crassirostris*, *Oithona davisae**, *O. nana**, *O. similis**, *Euterpina acutifrons***, *Microsetella norvegica***	Ueda (1991)
Sagami Bay, Honshu	*Acartia* spp., *Calanus sinicus*, *Clausocalanus* spp., *Ctenocalanus vanus*, *Lucicutia flavicornis*, *Paracalanus parvus* s.l., *Temora turbinata* (Calanoida only)	Shimode et al. (2006)
Suruga Bay, Honshu	*Acartia danae*, *A. omorii*, *Calanus sinicus*, *Canthocalanus pauper*, *Centropages tenuiremis*, *Clausocalanus furcatus*, *C. minor*, *Ctenocalanus vanus*, *Labidocera japonica*, *Paracalanus aculeatus*, *P. parvus* s.l., *Temora turbinata*, *Undinula vulgaris* (Calanoida only)	Itoh et al. (2005)
Seto Inland Sea, Honshu	*Acartia erythraea*, *A. omorii*, *A. pacifica*, *Acrocalanus gibber*, *A. gracilis*, *Calanopia thompsoni*, *Calanus sinicus*, *Centropages abdominalis*, *C. tenuiremis*, *Labidocera rotunda*, *Paracalanus parvus* s.l., *Parvocalanus crassirostris*, *Pontellopsis*	Hirota (1962, 1979) and Ohtsuka et al. (2004c)

(continued)

Table 22.1 (continued)

Location	Common species	References
	tenuicauda, *Pseudodiaptomus marinus*, *Tortanus forcipatus*, *T. gracilis*, *Oithona similis**, *O. davisae**, *Euterpina acutifrons***, *Microsetella norvegica***, *Corycaeus affinis****, *Oncaea venusta****	
Lake Nakaumi, Honshu	*Acartia hudsonica*, *A. sinjiensis*, *Eurytemora pacifica*, *Sinocalanus tenellus*, *Oithona davisae**	Ohtsuka et al. (1999)
Gokasho Bay, Honshu	*Acartia omorii*, *Parvocalanus crassirostris*, *Oithona davisae**	Hirakawa et al. (2006)
Shijiki Bay, Kyushu	*Acartia omorii* (as *A. clausi*), *A. steueri*, *Parvocalanus crassirostris*, *P. parvus* s.l., *Oithona brevicornis**, *O. nana**, *O. oculata**, *O. similis**, *O. simplex**, *Euterpina acutifrons***, *Microsetella norvegica***	Ueda (1980, 1982)
Omura Bay	*Acartia omorii*? (as *A. clausi*), *Centropages abdominalis*, *Paracalanus parvus* s.l., *Parvocalanus crassirostris*, *Pseudodiaptomus marinus*, *Oithona davisae**, *Microsetella norvegica***	Itoh and Iizuka (1979)
Yatsushiro Bay, Kyshu	*Acartia omorii*, *Paracalanus parvus* s.l., *Parvocalanus crassirostris*, *Oithona davisae** (as *O. nana*), *O. similis**, *Microsetella norvegica***, *Corycaeus* spp.***	Hirota (1975)
Ariake Sea, Kyushu	*Acartia erythraea, A. hudsonica, A. omorii, A. pacifica*, *Acrocalanus gibber*, *A. gracilis*, *Calanus sinicus*, *Paracalanus parvus* s.l., *Parvocalanus crassirostris*, *Pseudodiaptomus marinus*, *Temora turbinata*, *Tortanus forcipatus*, *Oithona attenuata**, *O. brevicornis**, *O. davisae**, *O. similis**, *O. simplex**, *Euterpina acutifrons***, *Microsetella norvegica***, *Corycaeus affinis****, *Oncaea clevei****, *O. media****, *Hemicyclops* sp.***	Beltrão et al. (2011)
River estuaries in western Japan	*Acartia ohtsukai, A. sinjiensis, A. tsuensis, Pseudodiaptomus inopinus, Sinocalanus tenellus, Oithona davisae**	Sakaguchi et al. (2011)
Sumiyo Bay, Amamioshima Island, Kyushu	*Acartia tsuensis*, *Pseudodiaptomus ishigakiensis*, *P. nansei* (as *P. inopinus*),	Oka and Saisho (1994)
Lagoons of Okinawa Island, Okinawa	*Acartia fossae*, *A. sinjiensis*, *Bestiolina similis*, *Oithona aruensis**, *O. attenuata* (stocky form)*, *O. dissimilis**, *O. oculata**, *O. simplex**	Ueda (2001)

(continued)

Table 22.1 (continued)

Location	Common species	References
Kabira Bay, Ishigakijima Island, Okinawa	*Acartia erythraea*, *A. fossae*, *A. steueri*, *Parvocalanus crassirostris*, *Oithina aruensis**, *O. dissimilis**, *O. oculata**, *O. simplex**	Nishida (1985)

No asterisk, Calanoida
*Cyclopoida
**Harpacticoida
***“Poecilostomatoida”

Blanco-Bercial (2013), the genera *Paracalanus* and *Parvocalanus* are paraphyletic and *Acrocalanus* is monophyletic. One of the dominant calanoids in coastal waters, *Paracalanus parvus* s.l., has been taxonomically confused since the beginning of Japanese planktology (see Table 22.1), and resembles *P. parvus*, *P. indicus*, and *P. quasimodo* (Hiromi, 1987). In Korean waters both *P. parvus* and *P. indicus* have been recorded (Kang 1996), but the former is suggested to have a restricted, high-latitude distribution in the North Atlantic (Hiromi 1987). Diagnostic features such as the morphology of the cephalosome and the presence/absence of a spinular row along the outer margin of the third exopodal segments of legs are highly variable even within a local population (Hiromi 1987), so a taxonomic revision of *Paracalanus*, including *P. parvus* s.l., is a high priority on a global scale.

The taxonomy of the coastal/oceanic family Calanidae was also confused, partly the result of low sexual dimorphism. The family was taxonomically revised by Russian copepodologists such as V.A. Jashnov and K.A. Brodsky, and more recently by Miller (1988) and Hulsemann (1994). The following species of *Calanus* and *Neocalanus* have been identified from Japanese waters: *C. pacificus*, *C. glacialis*, *C. sinicus*, *C. jashanovi*, *N. cristatus*, *N. gracilis*, *N. robustior*, *N. plumchrus*, and *N. flemingeri*. In Sagami Bay on the Pacific Coast of Honshu, the vertical distributions of copepodid stages of co-occurring *C. sinicus* and *C. jashanovi* were identified using genetic markers, revealing the presence of large populations of fifth copepodids of *C. sinicus* in the mesopelagic layer (Nonomura et al. 2008). Two sibling species, *N. plumchrus* and *N. flemingeri*, exhibit different annual life cycles in the North Pacific (Tsuda et al. 1999) and the Sea of Japan (Miller and Terazaki 1989) (see Fig. 22.6).

The taxonomy of the coastal/oceanic family Eucalanidae is also very difficult (Fleminger 1973). Geotze (2003) and Geotze and Ohman (2010) studied the molecular phylogeny and zoogeography of Eucalanidae and revealed that intraspecific genetic variation is found even in oceanic taxa, raising interesting questions concerning the nature of any biological barriers to gene flow in oceanic waters. Because calanids and eucalanids are considered not to have complex mating patterns (Tsuda and Miller 1998; Ohtsuka and Huys 2001), it is likely that sexual dimorphic features are less well developed.

As are marine taxa, freshwater taxa are more genetically differentiated than expected. Based on analyses using mitochondrial (mt) COI and nuclear internal transcribed spacers (ITS), Makino and Tanabe (2009) revealed that

Acanthodiaptomus pacificus on Japan's main islands consists of a cryptic species complex. They found genetic differentiation at a level of 15–22 % in mtCOI, among lineages corresponding to interspecific variation. Because freshwater habitats, in particular, subterranean waters, are generally more isolated from one another (Karanovic et al. 2013), such endemism as reported by Makino and Tanabe (2009) could be common.

Attention has been paid to the taxonomy and zoogeography of hyperbenthic calanoids, because they form a unique and diverse community just above the shallow- and deep-sea bed. This community contains both primitive and advanced taxa, suggesting complex colonization routes in the course of the calanoid evolutionary history (Ohtsuka 1999; Bradford-Grieve 2002, 2004). Shallow-water genera known from Japanese waters include *Metacalanus* and *Paramisophria* (Arietellidae); *Placocalanus* (Fig. 22.1b), *Pseudocyclops*, and *Ridgewayia* (Pseudocyclopidae); *Thompsonopia* (described as *Pseudocyclopia muranoi*) (Pseudocyclopiidae); and *Stephos* (Stephidae) (Tanaka, 1966; Ohtsuka, 1984, 1985, 1992, unpublished data; Ohtsuka and Hiromi 1987; Barr and Ohtsuka 1989; Ohtsuka et al. 1991, 1996b; Barthélémy et al. 1998). Deep-sea genera include *Bradyetes*, *Lutamator*, and *Paracommantena* (Aetideidae); *Sarsarietellus* and *Scutogerulus* (Arietellidae); *Macandrewella* (Scolecitrichidae); *Xanthocalanus* (Phaennidae); and *Tharybis* and *Neoscolecithrix* (Tharybidae) (Tanaka, 1960; Nishida et al. 1999; Ohtsuka et al., 2002, 2003, 2005b; Ohtsuka and Boxshall, 2004; Ohtsuka, unpublished data). Among them Pseudocyclopidae and Arietellidae are basal offshoots, whereas Aetideidae, Phaennidae, Scolecitrichidae, and Tharybidae are more terminal taxa (Bradford-Grieve et al. 2010, 2014; Blanco-Bercial et al. 2011).

22.2.3 Orders Poecilostomatoida and Cyclopoida: *Saphirella* Problem and Other Issues

The taxonomic position of the order Cyclopoida is unstable (Boxshall and Halsey 2004; Kim and Kim 2000; Huys et al. 2012; Tung et al. 2014). The order "Poecilostomatoida" was included within the Cyclopoida by Boxshall and Halsey (2004), but molecular analyses have shown that this conclusion is premature. "Poecilostomatoids" seem to be composed of several paraphyletic or polyphyletic groups (Kim and Kim 2000; Huys et al. 2012). In this chapter, we handle these orders separately.

Hemicyclops (Fig. 22.1e) and related genera belong to the family Clausidiidae of "Poecilostomatoida" and are recognized as a group basal to Cyclopoida and other poecilostomatoids (Huys et al. 2012). Small, enigmatic, planktonic poecilostomatoids called "*Saphirella*" have been recorded from brackish to oceanic waters (Itoh and Nishida 1991; Itoh 2006). Itoh and Nishida (1995, 2007, 2008) have elucidated that it includes the first copepodid stage of Clausidiidae, in particular, of *Hemicyclops*. Subsequent stages are loosely associated with benthic organisms such as crabs and polychaetes (Itoh and Nishida 2007, 2008). High abundance of "*Saphirella*"-like copepods or the first copepodid stage of clausidiids was recorded from Tokyo Bay, reaching about 5000 individuals/m^3 (Itoh 2006).

The taxonomy of Oncaeidae, a poecilostomatoid family in the mesopelagic community, has been revised by Böttger-Schnack and coworkers (Böttger-Schnack 2009; Böttger-Schnack and Schnack 2013, and references therein), including integrative molecular and morphological studies (Böttger-Schnack and Machida 2011). New genera, such as *Archioncaea*, *Triconia*, *Monothula*, and *Spinoncaea*, have been established, and the existing genera *Oncaea*, *Conaea*, and *Epicalymma* have been extensively revised. The Oncaeidae now includes 113 species (Razouls et al. 2015). When the oncaeid fauna of Japan was compiled by Itoh (1997) for an illustrated guide, it was based on the taxonomy before these revisions. Ecological studies in Tosa Bay (Nishibe et al. 2009), and the Kuroshio Extension area (Itoh et al. 2014) have recorded 45 and 35 oncaeid species, respectively.

New families and genera of "Poecilostomatoida" have been reported from invertebrate and fish hosts in Japanese waters, including Umazuracolidae (Fig. 22.1d) (Ho et al. 2006), Pseudohatschekiidae (Tang et al. 2010), *Biacanthus* (Tang and Izawa, 2005), and *Ttetaloia* (Uyeno and Nagasawa, 2012), all from fish. *Umazuracola* was originally established as the type of a monotypic family, but it was subsequently synonymized with the Taeniacanthidae (Huys et al. 2012). The enigmatic "poecilostomatoid" genus *Limnoncaea* Kokubo, 1914 found in plankton was recognized as an ergasilid, either *Ergasilus* or *Thersitina* (Ohtsuka et al., 2004a, b) (see Sect. 22.4.5: Life Cycle).

Three new species of the cyclopoid *Halicyclops* were described from estuaries of the Ariake Sea: *H. continentalis* as a continental relict and *H. uncus* and *H. ariakensis* as endemics (Ueda and Nagai 2009). New taxa of cyclopoids were found in marine invertebrates: *Chamicola* from bivalves (Ohtsuka et al. 2000a), *Loboixys* from ascidians (Ooishi 2006), and *Parenterognathus* and *Enterognathus* from comatulids (Ohtsuka et al. 2010, 2012). Sixty-one species of the cyclopoid family Cyclopidae, excluding groundwater species, were recognized from Japanese freshwaters by Ishida (2002).

The taxonomy and distribution of Oithonidae, representing the smallest but numerically dominant cyclopoids, in Suruga Bay and the Indo-Pacific oceanic waters were studied by Nishida et al. (1977) and Nishida (1985), respectively. These studies revealed that the species dominating in estuaries and embayment waters of Japan and previously reported as *Oithona nana* (e.g. Yamazi, 1955; Hirota and Hara, 1975) were *O. davisae* (see also Nishida and Ferrari, 1983 for taxonomic confusion among related species).

In Okinawan estuaries *Oithona dissimilis* is abundant, but two different size forms are distinguished (Ueda et al. 2011): the larger form is distributed in the lower estuaries (salinity, 25), and the smaller in the upper estuaries (around 7.5). These forms differ by 1.84–2.21 % in nuclear LSU rRNA and by 20.9–21.3 % in mtCOI, suggesting that *O. dissimilis* consititutes at least two cryptic species.

22.2.4 Other Orders: New Discoveries Continued

Two genera of the order Misophrioida are known from Japan: the deep-sea *Benthomisophria* and the hyperbenthic *Misophriopsis* (Tanaka, 1966; Ohtsuka et al., 1992). Misophrioids are not rare in the shallow and deep hyperbenthic communities (Ohtsuka, unpublished data), so undescribed taxa are likely to be discovered. Similar to Platycopioida and Calanoida, two new families, and many genera and species of misophrioids, have been discovered from marine caves worldwide (cf. Boxshall and Jaume 2000b).

Some new families and genera of the order Siphonostomatoida have been reported from invertebrate and fish hosts in Japanese waters: *Archidactylina* from hagfish (Izawa 1996), *Neomysidion* (Fig. 22.1i, j) from mysids (Ohtsuka et al. 2005a), and *Dangoka* from elasmobranchs (Izawa 2011). Molecular data (Freeman et al. 2013) support the proposal (Dojiri and Ho 2013) that *Pseudocaligus* is a junior synonym of *Caligus* (Fig. 22.1g).

A new genus of Monstrilloida, *Maemonstrilla* (Fig. 22.1h), was described from the Ryukyu Islands (Grygier and Ohtsuka 2008). *Maemonstrilla* (Japanese “mae” meaning anterior) bears anteriorly directed genital spines on the genital compound somite of the female, which are posteriorly directed in other monstrilloids. Because egg masses attached to the spines are positioned in a space surrounded by the right and left legs, Grygier and Ohtsuka (2008) regarded it as a kind of brood chamber. According to Huys et al. (2007), the Monstrilloida should be relegated to a family within the order Siphonostomatoida.

Taxonomy of benthic harpacticoids was led by Dr. T. Itô, who passed away in 1990. Since then, progress in harpacticoid taxonomy has been focused on freshwater (Ishida and Kikuchi 2000 and references therein) and phytal species (Takemori and Iwasaki 2009; Harris and Iwasaki 2009, and references therein). The biodiversity and community structure of deep-sea harpacticoids in Japanese waters have been extensively studied (Shimanaga et al. 2004, 2008; Kitahashi et al. 2013, 2014a, b).

22.3 Phylogeny and Zoogeography

22.3.1 Phylogeny of Copepods

Genetic analyses of copepods have generated insight into their origin, evolution, and zoogeography. Copepods are ‘eccentric’ in the organization of mitochondrial genes, and show low sequence similarity to those of other arthropods (55.1–57.5 %) (Machida et al. 2002). Although such information has been utilized to estimate phylogenetic relationships among higher taxa of Arthropoda (Boore et al. 1995), it appears inapplicable to copepods. In addition, deletion of a mitochondrial gene (ND6 protein-coding gene) can occur even within the calanoid genus *Neocalanus*

(Machida et al., 2006). The functional significance of such genetic abnormality is unknown.

The phylogeny of copepod orders is still under debate. The first offshoot, the order Platycopioida, is supported by morphology (Andronov 1974; Ho 1990, 1994a; Huys and Boxshall 1991). A genetic analysis of *Platycopia orientalis* is now in progress, which should allow the phylogenetic position of Platycopioida to be estimated more precisely (Tanaka et al., unpublished data).

Genetic analyses of the calanoid superfamilies support the morphology-based phylogeny of Andronov (1974) (Blanco-Bercial et al. 2011; Figueroa 2011; Bradford-Grieve et al. 2010, 2014). The molecular data indicate early divergence of the basal superfamilies Pseudocyclopoidea (including synonymized Epacteriscoidea), Diaptomoidea, and Arietelloidea from other superfamilies. The Pseudocyclopoidea is restricted to benthic layers, and is defined as a plesiomorphic taxon with an "underlying pattern of full development of arthrodial membranes between body somites and limb segments" (Bradford-Grieve et al. 2014).

A phylogeny of *Neocalanus* spp. by Machida et al. (2006) illustrates evolutionary processes in oceanic copepods (Ohtsuka et al. 2009b). The North Pacific lineage *Neocalanus flemingeri–N. plumchrus–N. cristatus* and the Antarctic circumpolar *N. tonsus* show a typical antitropical distributions; *N. gracilis* and *N. robustior* have a wide circumtropical distribution (Fig. 22.2a). The divergence and colonization of *Neocalanus* are deduced in accord with Cenozoic events (Machida et al. 2006; Ohtsuka et al. 2009b). The taxa showing antitropical distributions are characterized by adaptation to seasonal phytoplankton blooms and by ontogenetic vertical migration, consistent with their origin in the Oligocene. In addition, the existence of three Northern Hemisphere species suggests that speciation could have occurred in marginal seas after the Miocene.

Molecular phylogenetic analyses are informative for inferring relationships of highly modified parasitic copepods. Adult females of *Pectenophilus ornatus* infect the gills of the Japanese scallop as an endoparasite (Nagasawa et al. 1988) and resemble rhizocephalan barnacles. Molecular analysis by Huys et al. (2006), using nuclear 18S rDNA, revealed that it represents a highly transformed member of Mytilicolide of "Poecilostomatoida".

22.3.2 Zoogeography of East Asian Copepods

A comprehensive speciation pattern was proposed for the Indo-West Pacific coastal *Labidocera pectinata* species complex, based on vicariant events in accord with eustatic changes in sea level during the Pleistocene (Fleminger 1986). Such a vicariant mechanism is applicable to other Indo-West Pacific species groups, such as *Tortanus* (*Atortus*) species complexes, *Centropages alcocki* species group, *Labidocera detruncata* species complex, and *Pseudodiaptomus poppei* species subgroup (Ohtsuka and Kimoto 1989; Walter et al. 2002; Ohtsuka et al. 2005c, 2007b; Srinui et al. 2013; Hirabayashi and Ohtsuka 2014).

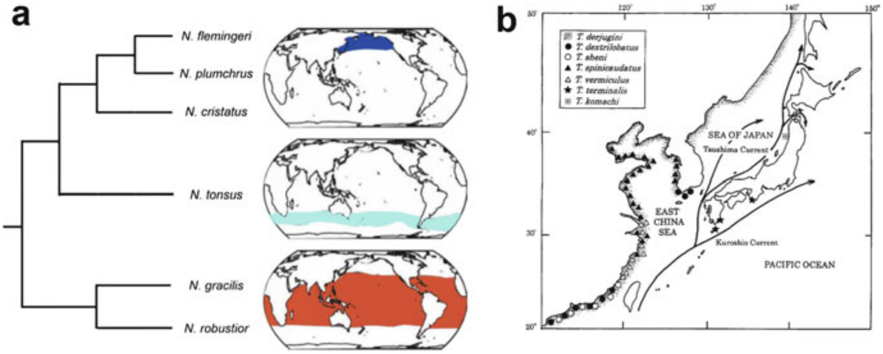

Fig. 22.2 Horizontal distributions of two groups of calanoid copepods. (**a**) Molecular phylogeny (*right*) and horizontal distributions (*left*) of the oceanic calanoid genus *Neocalanus* spp. (**b**) Distribution of seven species of the brackish/coastal calanoid subgenus *Tortanus* (*Eutoranus*) in East Asia. Note the distribution of *T.* (*E.*) *terminalis* along the Pacific coast of Japan (After Machida et al. 2006 (**a**); Itoh et al. 2001 (**b**); with permission from: Springer-Verlag (**a**); the Plankton Society of Japan (**b**))

The ancient East China Sea during the Pleistocene was considered as an enormous gulf of low-salinity water in glacial periods, and as a historic center of speciation for present-day brackish taxa (Nishimura 1981). All members of the subgenus *Tortanus* (*Eutortanus*) (Fig. 22.1c) originated from this gulf and were adapted to brackish water. The only exception, *T.* (*E.*) *terminalis*, is adapted to high-salinity water, and seems to have expanded its distribution eastward along the coast of Honshu Island (Fig. 22.2b), possibly because it had originated in high salinity near the mouth of the gulf (Ohtsuka and Reid 1998).

The Ariake Sea, western Kyushu, is known for its many benthic, nektonic, and planktonic continental relicts (Sato 2000). Planktonic relicts have been studied since the first report of *Sinocalanus sinensis* by Hiromi and Ueda (1987), followed by *Tortanus derjugini*, *Acartia ohtsukai*, and *Halicyclops continentalis*, the last two of which were described as new species (Ohtsuka et al. 1995; Itoh et al. 2001; Ueda and Bucklin 2006; Ueda and Nagai 2009).

Japanese freshwaters lie within the Palaearctic region that accommodates 134 genera and 1204 species of copepods, the most speciose freshwater region in the world (Boxshall and Defaye 2008). This area is characterized by a wide species diversity of Cyclopidae (29 %), Canthocamptidae (27 %), and Diaptomidae (12 %), and by the greatest species and family richness of fish parasites.

Freshwaters have been repeatedly colonized by copepods since the Paleozoic (Ho 1994b; Boxshall and Jaume 2000a). Wyngaard et al. (2010) studied the phylogeny and zoogeography of *Mesocyclops* from the Old and New Worlds to infer possible colonization routes. The monophyly of Old World taxa and the paraphyly of New World taxa are clear in their analysis. Three hypotheses are proposed for the origin and dispersal of *Mesocyclops* since the Cretaceous: New World origin, Laurasian origin, and West Gondwana origin. Surprisingly, even in a single species, *Eurytemora affinis*, rapid and repeated colonization from marine to freshwater habitats has occurred (Lee 1999). Makino and Tanabe (2009) found that Japanese populations of the freshwater *Acanthodiaptomus pacificus* are genetically differentiated, comprising three lineages and showing a parapatric distribution. Such divergence can be related to marine transgression and regression events, and to introgressive hybridization during the Miocene.

22.4 Ecology

22.4.1 Population Dynamics

Population dynamics of numerically important species of freshwater and marine planktonic copepods have been intensively studied. In the Seto Inland Sea, population dynamics of coastal species of calanoids, cyclopoids, and harpacticoids have been investigated by Uye and colleagues (Uye and Sano 1995, 1998; Lian and Uye 1996a, b; Lian et al. 1996; Uye et al. 2002). These studies revealed high mortality in calanoid populations during the egg stage or early stages by predation or cannibalism. In the northwestern Pacific, the ontogenetic migration and life cycles of large-sized particle-feeders such as *Neocalanus* spp. and *Eucalanus bungii* have been surveyed by Miller and Terazaki (1989), Kobari and Ikeda (2001), and Tsuda et al. (2004). These copepods are adapted to phytoplankton blooms and diapause in deep layers during non-bloom seasons (see Fig. 22.6). *Eucalanus bungii* and *Neocalanus flemingeri* exhibit biennial life cycles in the Oyashio region (Kobari and Ikeda 2001; Tsuda et al. 2004).

Life cycles of some numerically important, freshwater calanoid and cyclopoid copepods have been investigated, and special attention was paid to dormancy of eggs and copepodids (Ban 1992, 1998; Ban and Minoda 1994; Kobari and Ban 1998).

Life histories of two clausidiid copepods, *Hemicyclops gomsoensis* and *H. spinulosus* associated with invertebrate burrows, were studied in the Tama River estuary, demonstrating the significance of burrow association in generating and maintaining species diversity in mudflats (Itoh and Nishida 2007, 2008).

Recent studies have pointed out that the population dynamics of copepods are strongly influenced not only by their predators but also by parasites and parasitoids (Ianora et al. 1987; Kimmerer and McKinnon 1990; Ho and Perkins 1985; Ohtsuka et al. 2000c, 2004c, 2007a, 2011a).

22.4.2 Distribution of Marine and Brackish Planktonic Copepods in Japan

The current systems in the seas around Japan are complex and influence the horizontal and vertical distributions of free-living and symbiotic copepods. The cold Oyashio and the warm Kuroshio/Tsushima Currents (see Fig. 22.2b) are each well characterized by planktonic indicators (Ohtsuka and Ueda 1999). A unique phenomenon is the submergence of the Oyashio Current in Sagami Bay, where the Kuroshio is prevalent in the upper layer, and is characterized by the occurrence of deep populations of the cold-water species *Neocalanus cristatus* (Omori, 1967; Oh et al., 1991). The composition and abundance of copepods in a warm core originating from the Kuroshio were compared with those in adjacent waters of the Oyashio off northeastern Japan (Hattori 1991). The warm core strongly influenced the distributional patterns of copepods, and cold-water species such as *N. cristatus* and *Eucalanus bungii* avoided the core (Hattori 1991).

The book *An Illustrated Guide to Marine Plankton in Japan* (Chihara and Murano 1997), containing illustrated keys to species of copepods occurring in Japanese and adjacent waters, contributed much to the enhancement of ecological research in the region.

Seasonal changes in species composition and abundance of planktonic copepods in Japanese coastal waters have been intensively studied (Table 22.1). Coasts influenced by Oyashio waters are characterized by cold-water species such as *Acartia longiremis*, *A. omorii*, *A. steueri*, *Eurytemora pacifica*, *Pseudocalanus newmani*, and *Oithona similis*. Coasts adjacent to the Kuroshio Current are distinguished by warm-water species such as *Calanus sinicus*, *Parvocalanus crassirostris*, *Paracalanus parvus* s.l., *Temora turbinata*, *Labidocera japonica*, *Corycaeus affinis*, and *Microsetella norvegica*. Inlet and brackish waters in the main islands of Japan are dominated by *Acartia sinjiensis*, *A. hudsonica*, *A. erythraea*, *A. tsuensis*, *Parvocalanus crassirostris*, *Sinocalanus tenellus*, *Pseudodiaptomus inopinus*, *P. marinus*, *Oithona davisae*, and *Euterpina acutifrons*. In the Nansei Islands, brackish areas are characterized by *Acartia tsuensis*, *Pseudodiaptomus ishigakiensis*, *P. nansei*, and *Oithona dissimilis*. The horizontal zonation of planktonic copepods (Fig. 22.3) is determined by combinations of water temperature, salinity, food concentration, and predation pressure (Ueda 1991, 2001).

Extremely high abundances of *O. davisae* were recorded in the Ariake Sea (Hirota 1990), Lake Nakaumi (Ohtsuka et al. 1999), and Tokyo Bay (Itoh et al. 2011; Itoh and Nishida 2015), reaching about 1 million individuals/m^3 Some coastal calanoids such as *Acartia*, *Labidocera*, *Pontella*, and *Tortanus* (*Atortus*), and cyclopoids such as *O. oculata* form dense swarms or schools during the daytime and disperse at night (Ueda et al. 1983; Kimoto et al. 1988; Ohtsuka et al. 2000b).

In subarctic to subtropical coastal waters of Japan, seasonal succession in planktonic copepod communities is remarkable, and it reflects combinations of

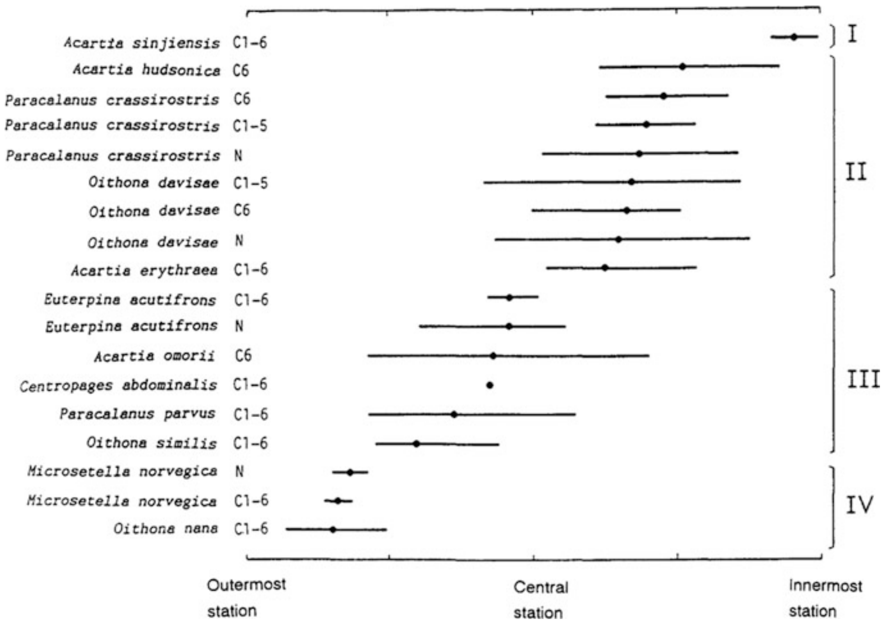

Fig. 22.3 Distribution ranges of abundant planktonic copepods in Maizuru Bay, western Japan. *Horizontal lines* and *circles* represent distribution ranges in the bay during the period of high abundance and their mean points, respectively. *C1–C6* first to sixth copepodid stages, *N* naupliar stages, *I–IV* copepod communities represented by indicator(s) (After Ohtsuka and Ueda 1999, with permission from the Plankton Society of Japan)

seasonal changes in water temperature, salinity, inflow of currents, foods, and other environmental factors. Some brackish and coastal diaptomoidean taxa such as *Acartia*, *Centropages*, *Labidocera*, and *Tortanus* produce resting eggs at the beginning of a period unfavorable for planktonic adults, which diapause in sediments (Uye 1985; Ban 1998).

In Lakes Nakaumi and Shinjiko, *Sinocalanus tenellus* aggregates just above the pycnocline (Harada et al. 1985). The mechanism by which positioning of planktonic copepods is maintained during flooding in estuaries was clarified by Ueda et al. (2004). Two brackish species, *Sinocalanus sinensis* and *Pseudodiaptomus inopinus*, aggregated just above the bottom in submerged channels outside the mouth during heavy flooding. Losses from the populations, in particular of immature copepodids, were compensated by reproduction after the flood.

In oceanic calanoids and oncaeid copepods, niche partitioning by vertical habitat or food is conspicuous irrespective of feeding habits (Yamaguchi et al. 2002; Kuriyama and Nishida 2006; Nishibe et al. 2009; Matsuura et al. 2010; Sano et al. 2013, 2015; Itoh et al. 2014). Each species of the detritivorus family Scolecitrichidae (Nishida and Ohtsuka 1997) showed a specific combination of body size, vertical distribution, and diel migration pattern in the epipelagic and mesopelagic zones of Sagami Bay (Kuriyama and Nishida 2006) (Fig. 22.4,

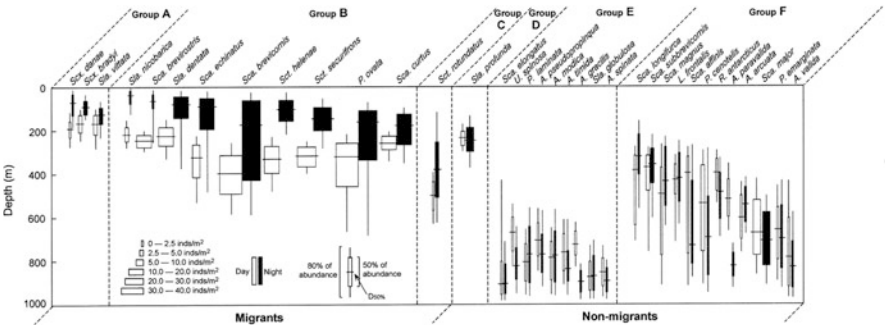

Fig. 22.4 Vertical distributions and abundance of the family Scolecitrichidae in Suruga Bay, middle Japan. The width of the *box* denotes the density of 50 % of the population between 25 and 75 % distributional depth. Abbreviated generic names: *A Amallothrix*, *L Lophothrix*, *R Racovitzanus*, *Sca Scaphocalanus*, *Sla Scolecithricella*, *Sct Scolecithrix*, *U Undinothrix*. See Table 22.2 for grouping. (After Kuriyama and Nishida 2006, with permission from Koninklijke Brill NV)

Table 22.2). These scolecitrichids co-exist by segregation in spatiotemporal distributions, antipredation behaviors, and diet. Carnivorous species of *Euaugaptilus* in the Sulu Sea and Celebes Sea similarly showed segregation in vertical distribution and food niche (Matsuura et al. 2010). *Oncaea* also exhibited body size-dependent niche separation in the upper 200 m in the Kuroshio Extension region, and the population size was correlated with appendicularian abundance (Itoh et al. 2014); this is explained by the feeding of oncaeids on phyto- and zooplankers retained on discarded appendicularian houses (Alldredge 1972; Ohtsuka and Kubo 1991; Ohtsuka et al. 1993, 1996a; Nishibe et al. 2015).

Molecular techniques can be applied in the analysis of copepod community structure. Hirai et al. (2013) recommended ITS2 and 28S rDNA as molecular markers for calanoids and detected high intraspecific variability in subtropical waters. Hirai et al. (2015) estimated species richness and abundance of planktonic copepods using a metagenomic approach. Such innovative techniques can be highly effective in understanding community structure.

22.4.3 Feeding: Highly Complex Feeding Habits in Oceanic Regions

High-speed cinematographic studies have revealed that particle-feeding calanoids employ suspension-feeding rather than filter-feeding (Koehl and Strickler 1981; Paffenhöfer et al. 1982). In addition, carnivory and detritivory have also been revealed in a wide variety of planktonic copepods (Nishida et al. 1991; Ohtsuka and Kubo 1991; Ohtsuka et al. 1993, 1997; Nishida and Ohtsuka 1996, 1997; Nishida et al. 2002; Sano et al. 2013). Feeding of planktonic copepods has been

Table 22.2 Groups of the Scolecitrichidae in Suruga Bay, central Japan, based on vertical distribution and diel migration pattern

Group	Ecological definition
A	Epipelagic migrants: migrant with major population in the upper 200 m both day and night
B	Interzonal migrants: migrant with major population in the upper 200 m at night and below 200 m in the daytime
C	Upper mesopelagic migrants: migrant with major population in the upper mesopelagic zone (200–400 m) both day and night
D	Upper mesopelagic non-migrants: non-migrant with major population in the upper mesopelagic zone (200–400 m)
E	Lower mesopelagic species: species with major population below 700 m
F	Mesopelagic species: species with a broad range below the 200-m layer

From Kuriyama and Nishida (2006)

intensively investigated by Japanese copepodologists since Anraku and Omori (1963) and Itoh (1970). The amazing feeding habits of oceanic calanoids have been revealed by Japanese researchers (Ohtsuka and Onbé 1989; Nishida et al. 1991, 2002; Ohtsuka and Kubo 1991; Nishida and Ohtsuka 1996, 1997; Ohtsuka and Nishida 1997; Ohtsuka et al. 1997; Matsuura and Nishida 2000; Sano et al. 2013). Specialized carnivory and detritivory are found mainly in oceanic waters.

Heterorhabdus (Fig. 22.5a) and related genera have a pair of fangs on the mandibular gnathobases (Nishida and Ohtsuka 1996). Venom or anesthetic is released from two glandular cells via paired pores on the posterior surface of the labrum (Fig. 22.5b). These glands may be modified salivary glands homologous with those of particle-feeding heterorhabdids such as *Disseta* and *Mesorhabdus* (Ohtsuka et al., 1997). Some augaptilid genera have specialized ‘button setae’ on the maxillae and maxillipeds, which may function as shock absorbers during prey capture (Matsuura and Nishida 2000). Candaciids carry heavily chitinized, sword-like elements on the maxillae, which are remarkably different from those of carnivores such as Euchaetidae, Pontellidae, and Tortanidae (Ohtsuka et al. 1987; Ohtsuka and Onbé 1991). *Candacia* is specialized for predation on gelatinous zooplankters such as appendicularians (Ohtsuka and Onbé 1989; Ohtsuka and Kubo 1991).

Detritivory is known in the so-called Bradfordian families such as Phaennidae, Scolecitrichidae, and Tharybidae (Nishida and Ohtsuka 1997; Nishida et al. 2002). The maxillae, maxillipeds, and rarely, maxillules bear special chemosensory elements to detect detrital material. Essentially two types of chemosensors are recognized: worm-like and brush-like setae (Nishida and Ohtsuka 1997). Based on ultrastructure, the former may be a general sensor and the latter a specific one. In addition to mouthpart chemosensors, the phaennid *Cephalophanes* has highly developed naupliar eyes (Fig. 22.5c) that may be used to detect crustacean detrital material via associated bioluminescent bacteria (Nishida et al. 2002).

Non-calanoids, such as *Oithona* and *Oncaea*, have been shown to exhibit different feeding habits by Japanese copepodologists. *Oithona davisae* prefers

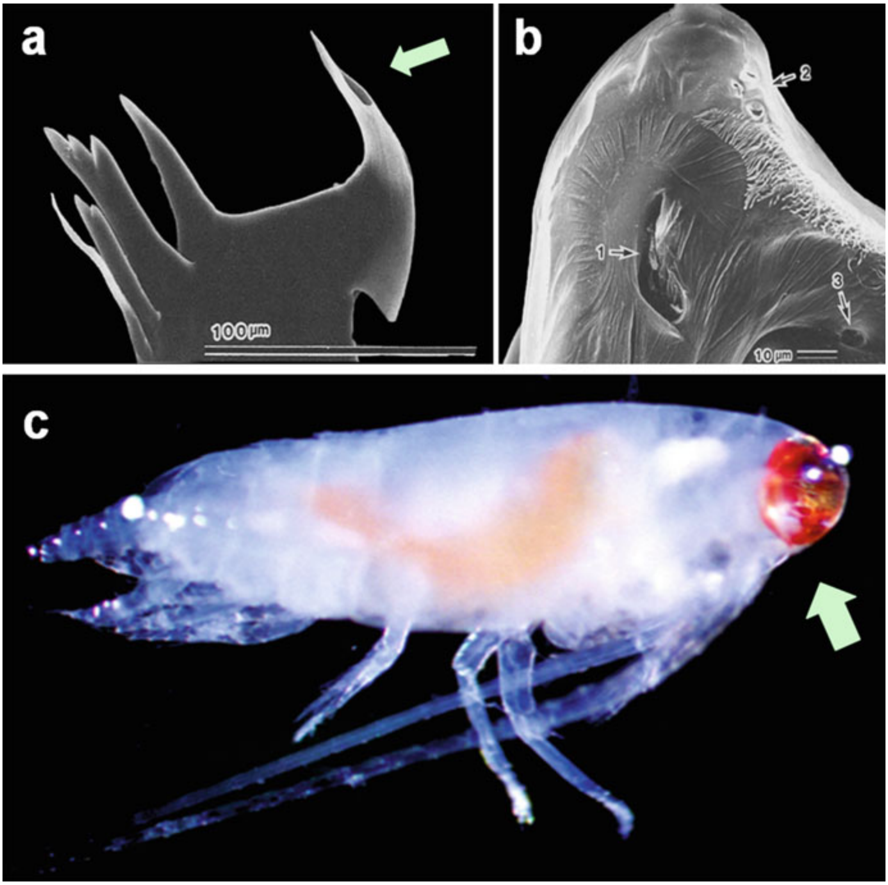

Fig. 22.5 Specialized feeding strategies of deep-sea calanoids. (**a**) Mandibular cutting edge of specialized carnivorous genus *Heterorhabdus*, hypodermic needle-like structure (*arrowed*). (**b**) Openings of the venom gland (*1*) and other secretory glands (*2*, *3*) on posterior surface of the labrum of *Heterorhabdus*. (**c**) Specialized detritivore *Cephalophanes*, lateral view, large reddish naupliar eye (*arrowed*) (After Nishida and Ohtsuka, 1996 (**a**, **b**): with permission from Springer-Verlag)

dinoflagellates to diatoms (Uchima 1988). *Oncaea* and related genera are associated with discarded appendicularian houses, feeding on plankters retained on the appendicularian feeding nets (Ohtsuka and Kubo 1991; Ohtsuka et al. 1993, 1996a).

22.4.4 Reproduction

The copulatory behavior of coastal, diaptomoidean calanoids such as *Centropages*, *Labidocera*, and *Pseudodiaptomus* has been well studied by western copepodologists (cf. Blades and Youngbluth 1979). However, those of more derived oceanic taxa (non-diaptomoideans) were unknown before Tsuda and Miller (1998) observed mating behavior of *Calanus marshallae*. Diaptomoideans have a geniculate right antennule in males and need several tens of minutes to complete the copulatory process (duration from grasping of mate to attachment of spermatophore) (Ohtsuka and Huys 2001). In contrast, advanced calanoids lack geniculate antennules and expend only 0.1 s to a few seconds in copulation (Tsuda and Miller 1998), which is interpreted as an antipredation strategy of the advanced taxa [=Myelinata sensu Lenz (2012)] with myelinized nerve fibers (Tsuda and Miller 1998; Ohtsuka and Huys 2001; Lenz 2012). A mating plug was first observed in a diaptomoidean copepod *Tortanus* (*Atortus*) (Ohtsuka and Huys, 2001; Barthélémy et al., 2003).

Bioluminescence is reported in some oceanic calanoids, harpacticoids, and "poecilostomatoids" (Herring, 1988) and may be involved in mating, antipredation, and warning behaviors (Herring 1988, 2007; Herring et al. 1993; Takenaka et al. 2013). The evolution of genes coding luciferase in the oceanic Arietelloidea and their adaptive significance are explored by Takenaka et al. (2013).

Mating behavior of the planktonic cyclopoid *Oithona davisae* was observed by Uchima and Murano (1988). This behavior differs from that of calanoids in precopulatory spiraling by the male in search of a mate and to diffuse the pheromone released from the female; grasping of specialized setae on female leg 4 by both antennules of the male. The function of the special "cephalosome flap organ" (Nishida 1986) located laterally on the male cephalothorax is not clear but may be involved in perception of hydrodynamic disturbance or sex pheromones during spiraling.

Sea sapphires or males of the "poecilostomatoid" genus *Sapphirina* (Fig. 22.1f) are unique in having beautiful, species-specific iridescence caused by the multiple layers of hexagonal guanine platelets in the epidermal cells (Chae and Nishida 1994). The specific colors of the males may be involved in mating (Chae and Nishida 2004).

Precopulatory mate-guarding was investigated in the shallow-water interstitial harpacticoid *Phyllopodopsyllus* sp. (Shimanaga and Shirayama, 2005): the adult male mainly grasps the fifth and fourth copepodid stages of the female. They noted a significant correlation between the population density and the number of precocious couples.

22.4.5 Life Cycle

Diapause in freshwater and marine planktonic copepods was intensively studied in Japan in the 1970s–1990s. It is classified into three categories: egg, naupliar, and copepodid dormancy (Ban 1998). Egg dormancy is common in freshwater, brackish, and marine calanoids (Uye 1985; Ban 1998; Ohtsuka et al. 1999); copepodid dormancy is found in freshwater cyclopoids (Kobari and Ban 1998) and oceanic

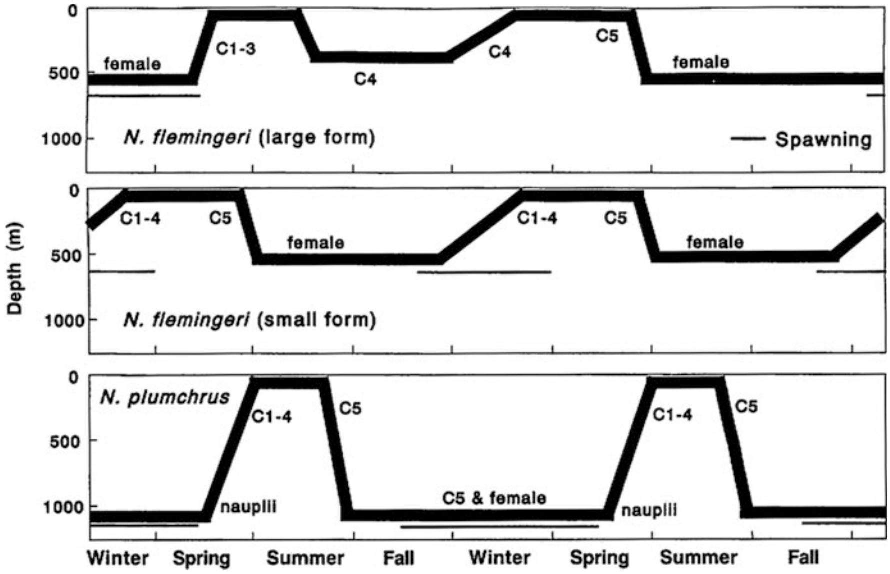

Fig. 22.6 Ontogenetic migration and biennial life cycle of the oceanic calanoids, *Neocalanus flemingeri* (small and large forms) and *N. plumchrus*, in the Oyashio region. Phytoplankton bloom occurred in April and May. *C1–C5* first to fifth copepodid stages (After Tsuda et al. 2001, with permission from the Plankton Society of Japan)

calanoids (Miller and Terazaki 1989; Kobari and Ikeda 2001; Tsuda et al. 2004). Naupliar dormancy is known from the Antarctic calanoid *Paralabidocera antarctica* (Tanimura et al., 1996). As *Neocalanus* spp. and *Eucalanus bungii* are pivotal import members of the North Pacific ecosystem, their life cycles have been investigated by Japanese copepodologists (Miller and Terazaki 1989; Tsuda et al. 1999, 2001, 2004; Kobari and Ikeda 2001). They showed that spawning, growth, and diapause occur in concert with phytoplankton blooms, and that spatiotemporal partitioning was apparent among these large-sized particle-feeders (Fig. 22.6).

The life cycle of sea lice (Caligidae) such as *Caligus* and *Lepeophtheirus* has been clarified. This is a vitally important discovery, because the developmental stages of these pathogenic copepods were confused. In *Caligus*, two naupliar, one (infective) copepodid, and four chalimus stages are distinguished before adults, whereas in *Lepeophtheirus*, two naupliar, one copepodid, two chalimus, and two preadult stages are differentiated (Ohtsuka et al. 2009a; Venmathi Maran et al. 2013). Chalimi and preadults are clearly defined as postnaupliar stages between the infective copepodid and adult (Venmathi Maran et al. 2013). The number of postnaupliar (= copepodid) stages of sea lice is identical to that of other copepods (six stages, including adults) (Huys and Boxshall 1991).

In *Caligus fugu*, the site specificity of developmental stages is remarkable: copepodids infect fins of host puffer fish, and then metamorphose to chalimi firmly attached to the fin via a frontal filament, while adults temporarily attach to the host body surface using paired lunules and the cephalothoracic sucker, and can move freely over the host (Ohtsuka et al. 2009a; Tasumi et al. 2015). The lunules are derived as modifications of the dorsal membrane along the margin of the paired frontal plates (Kaji et al. 2012).

More attention is now paid to pelagic adult sea lice, because some records of their occurrence in plankton seem not to be accidental (Ho and Lin 2004; Venmathi Maran and Ohtsuka 2008; Venmathi Maran et al. 2012b, c). For example, both sexes of *Caligus undulatus* have never been found on any fish host (Ho and Lin 2004; Venmathi Maran and Ohtsuka 2008; Suarez-Morales et al. 2012; Venmathi Maran et al. 2012b, c). There are similarities with the life cycle of some freshwater and brackish Ergasilidae (Ohtsuka et al. 2004a, b) in which adult females frequently detach from the host and swim freely in the water column.

22.4.6 Alien Problem

The introduction of alien copepods has resulted in elimination of native species, economic losses in aquaculture, and devastation of indigenous ecosystems (Fleminger and Kramer 1988; Orsi and Ohtsuka 1999; Ohtsuka et al. 2004d, 2008, 2011b; Ohtsuka and Hiromi 2009; York et al. 2014). Planktonic and benthic copepods have been introduced via ballast water or as contamination in the international trade of aquatic products (Ohtsuka et al. 2004d, 2008, 2011b). Parasitic copepods have been introduced via the international trade of aquatic products or pets (Ohtsuka et al. 2004d). No introductions of alien planktonic and benthic copepods in Japan have as yet been reported, partly because Japan is referred to as an exporter of ballast water based on foreign trade statistics (Ohtsuka et al. 2008; Ohtsuka and Hiromi 2009). Our molecular analysis suggests that the calanoid *Pseudodiaptomus marinus* has most likely been introduced from Japan to San Francisco Bay via ballast water (Ohtsuka et al. 2011b; Shimono et al., unpublished data). East Asian copepods have also been reported from European waters: *Pseudodiaptomus marinus* from the North Sea (Brylinski et al. 2012) and *Oithona davisae* from the Mediterranean (Saiz et al. 2003), the Black Sea (Temnykh and Nishdia 2012), and the North Sea (Cornils and Wend-Heckmann 2015).

The parasitic copepod *Caligus sclerotinosus* (Fig. 22.1g) has spread over western Japan since Ho et al. (2004) reported it in Oita Prefecture. It was originally described from the gilthead sea bream *Pagrus auratus* in Australia and has likely been introduced to farming areas of red sea bream *P. major* in western Japan through the import of fish seed (Ho et al. 2004; Nagasawa et al. 2010; Ohtsuka 2010). The endoparasitc copepod *Mytilicola orientalis* has been introduced from Japan to Europe and the Pacific Coast of North America via transplantation of the cultured oyster *Crassostrea gigas* and has reinfected commercial and noncommercial native bivalves in Europe (Stock 1993; Steele and Mulcahy 2001).

Ueda and Ishida (1997) surveyed the freshwater copepod fauna in Okinawa from 1984 to 1991, compared with the results of a survey by F. Kiefer more than 50 years ago. Larger copepods such as *Mesocyclops* had disappeared, but smaller *Thermocyclops crassus* was dominant, which they suggested might have been a result of eutrophication and the introduction of planktivorous African cichlids.

22.5 Fisheries

22.5.1 Copepods as Prey for Fish

Relationships between feeding behavior of fish juveniles and the distribution of planktonic copepods have been investigated in the mouth of Chikugo River, Kyushu. Larvae and early juveniles of Japanese temperate bass *Lateolabrax japonicus* migrate to the turbid, low-salinity area of the river, where they prey upon the abundant calanoid *Sinocalanus sinensis* (Hibino et al., 1999; Suzuki et al., 2008). Larvae of two species of tongue sole *Cynoglossus* have different vertical distribution patterns in concert with tides, but both preferably feed on the benthic harpacticoid *Pseudobradya* sp. (Yagi et al., 2009).

Calanoid and cyclopoid copepods such as *Acartia*, *Tortanus*, and *Oithona* form dense swarms near the bottom exclusively during the daytime (Ueda et al. 1983; Kimoto et al. 1988; Ohtsuka and Kimoto 1989; Ohtsuka et al. 2000b). Swarming is considered to be an anti-predation strategy. However, early juveniles of red sea bream *Pagrus major* and crimson sea bream *Evynnis japonica* feed primarily on planktonic copepods such as *Acartia* from the near-bottom (Kiso 1981, 1982). Anti-predation from gobies by inhabiting burrows has been suggested for the poecilostomatoid *Hemicyclops gomsoensis* by field and experimental observations (Itoh and Nishida 2013).

22.5.2 Copepods Parasitic on Cultured Fish

Caligids are well known as fish pests causing economic losses in marine fish farms. Pathogenic species in Japan include *Caligus fugu* on tiger puffer *Takifugu rubripes*; *C. longipes* on striped jack *Pseudocaranx dentex*; *C. orientalis* on rainbow trout *Onchorhynchus mykiss*; *C. sclerotinosus* on red sea bream *Pagrus major*; *C. spinosus* on yellowtail *Seriola quinqueradiata*; *Lepeophtheirus longiventris* on spotted halibut *Verasper variegatus*; and *L. paralichthydis* on olive flounder *Paralichthys olivaceus* (Ogawa, 1996; Nagasawa, 2004; Lester and Hayward, 2006; Ohtsuka et al., 2009b, unpublished data). The pennellid copepod *Peniculus minuticaudae* infects fins of thread filefish *Stephanolepis cirrhifer* and has expanded its distribution in western Japan and Korea (Venmathi Maran et al. 2012a; Ismail et al. 2013). These ectoparasites infect fins and skin of host fishes and cause inflammation, anemia, osmoregulatory failure, and secondary bacterial infection (Lester and Hayward 2006). The salmon louse *Lepeophtheirus salmonis* causes heavy mortality of cultured Atlantic salmon *Salmo salar* in Europe and North America, but not in Japan (Nagasawa 2004). Coho salmon *O. kisutch* cultured in Japan is immunologically more resistant to the parasitism by caligids (Nagasawa 2004).

In freshwater aquaculture in Japan, the “poecilostomatoid” family Ergasilidae, the “cyclopoid” family Lernaeidae, and the siphonostomatoid family Lernaeopodidae are recognized as pests (Johnson et al. 2004; Piasecki et al. 2004; Nagasawa et al. 2007).

22.5.3 Copepods Parasitic on Commercially or Ecologically Important Invertebrates

A highly modified copepod *Pectenophilus ornatus* is endoparasitic on the gills of Japanese scallop *Mizuhopecten yessoensis*. It is pathogenic in culture areas of northern Japan (Nagasawa et al. 1988; Suzuki and Matsutani 2009). Its prevalence on juvenile scallops reached 100 % in Miyagi Prefecture, northern Honshu (Suzuki and Matsutani 2009). In China, mass mortality of the cultured hard clam *Meretrix meretrix* was caused by the “poecilostomatoid” *Ostrincola koe* (Ho and Zhang, 1994), which is widely distributed in East Asia including Japan, and shows a wide host specificity (Kim and Sato 2010).

The life cycle and ecology of the nicothoid copepod *Neomysidion rahotsu* (Fig. 22.1i, j) parasitic on mysids was studied in the Seto Inland Sea (Ohtsuka et al. 2005a, 2007a, 2011a). The infection impacts fertility, because adult females prey upon host eggs in the marsupium. Interestingly, another parasite *Prodajus curviabdominalis* (Dajidae, Isopoda) utilizes the same host and site and possibly shows the same feeding habit. The two parasites alternate in their seasonal occupation of the host’s marsupium and, as a result, the host mysid is constantly infected throughout the year. Another nicothoid copepod *Choniomyzon inflatus* was described from the external egg masses of a commercially important fan lobster *Ibacus novemdentatus*, although its feeding habits are unknown (Wakabayashi et al. 2013).

22.6 Conclusions

Studies on the copepod biodiversity in Japanese waters are summarized as follows.

1. The species diversity of marine and freshwater planktonic copepods has been well resolved in Japanese waters since the pioneering studies of the late Drs. H. Marukawa, T. Sato, and S. Kokubo in the Taisho era (the 1910s), whereas benthic and symbiotic taxa urgently need more intensive survey. Symbionts,

especially on invertebrates, are poorly known in Japan. Cavernicolous and hyperbenthic copepods have been given less attention than in Western countries, although some have shed light on important phylogenetic and zoogeographic events.

2. Seas surrounding Japan are strongly influenced by a combination of the Kuroshio and Oyashio Currents, resulting in high species richness. These waters are zoogeographically complex, composed of a mixture of the Indo-West Pacific and East Asian elements, followed by the Okhotsk–Bering and Arctic–North Atlantic ones, in coastal waters, Tethyan relicts in the subtropical regions, and continental relicts in the Ariake Sea. The East Asian elements have originated from the ancient East China Sea since the Miocene. Freshwater taxa are essentially Palaearctic.
3. Molecular studies have revealed the presence of cryptic and sibling species within common species and demonstrated the unique mitochondrial gene arrangements of copepods. Molecular techniques have become a powerful tool for rapidly estimating species composition and biomass of copepod communities.
4. The ecological attributes of copepods in Japanese waters are diverse, in response to the complex environments. Distinct seasonal changes are reflected in the complicated life cycles of marine and freshwater copepods: ontogenetic vertical migration or dormancy at the population level and succession and interspecific interactions at the community level.
5. The biology of deep-sea copepods has been intensively studied in Japanese waters. Special sensory and feeding organs of planktonic detritivores and carnivores have been revealed in taxa inhabiting deep waters off Japan. Habitat and food resource partitioning or niche separation is conspicuous in deep-sea planktonic copepods, irrespective of taxonomic group and feeding habit.
6. Brackish-water copepods, especially those inhabiting river mouths, have special strategies for population maintenance. Some brackish calanoids are very abundant and are important prey items for juveniles of commercially important fish.
7. Aquaculture is intensive in Japan, where serious problems are caused by parasitic copepods such as caligids and pennellids. Alien parasites have been introduced to Japan and are now spreading. Planktonic copepods have also been introduced from Asian countries to other regions via ballast water. Because some of them are regarded as invasive aliens with the capacity to impact indigenous ecosystems drastically, the ballast water management of the International Maritime Organization (IMO) should become effective as soon as possible.

22.7 Perspectives

Molecular techniques have driven rapid advances in copepodology. However, as many copepodologists have already noticed (Mauchline 1998), simple microscopic observations are still necessary. The taxonomic identity of the dominant planktonic species *Paracalanus parvus* s.l. on the Japanese coasts still awaits clarification. Because copepods are one of the most abundant metazoans on Earth, and are directly or indirectly related to human beings, the taxonomy, ecology, and physiology of copepods should be more intensively studied with regard to changes in global environments. In addition, we should better utilize copepods from a biomimetic aspect, as Benuys (1997) insists that biomimetics is essential to create sustainable human societies in the future. In particular, their optical and chemical sensors are so acute and compact that these could be biomimetic applications. In addition, the mystery of the rearrangement of mitochondrial genes in copepods should be solved.

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References

Alldredge AL (1972) Discarded appendicularian houses as sources of food, surface habitats, and particulate organic matter in planktonic environments. Limnol Oceanogr 21:14–23

Andronov VN (1974) Phylogenetic relations of large taxa within the suborder Calanoida (Crustacea, Copepoda). Zool Zh 53:1002–1012

Anraku M, Omori M (1963) Preliminary survey of the relationship between the feeding habit and the structure of the mouth-parts of marine copepods. Limnol Oceanogr 8:116–126

Arbizu PM (1997) *Sarsicopia polaris* gen. et sp. n., the first Platycopioida (Copepoda: Crustacea) from the Arctic Ocean, and its phylogenetic significance. Hydrobiologia 350:35–47

Asami H, Shimada H, Ishida R, Takayanagi S (2010) Interannual variabilities of a few dominant copepods abundances during spring in Ishikari Bay, western Hokkaido, Japan. Sci Rep Hokkaido Fish Exp Stn 77:1–11 (in Japanese with English abstract)

Ban S (1992) Seasonal distribution, abundance and viability of diapause eggs of *Eurytemora affinis* (Copepoda: Calanoida) in the sediment of Lake Ohnuma, Hokkaido. Bull Plankton Soc Jpn 39:41–48

Ban S (1998) Dormancy in Copepoda. Umi no Kenkyu 7:21–34 (in Japanese with English abstract)

Ban S, Minoda T (1994) Seasonal distribution of *Eurytemora affinis* (Poppe, 1880) (Copepoda; Calanoida) in freshwater lake, Ohnuma, Hokkaido. Bull Fac Fish Hokkaido Univ 40:147–153

Ban S, Miyagawa Y, Okuda Y, Shiga N (1998) Succession of the calanoid copepod community in Funka Bay during spring phytoplankton bloom. Mem Fac Fish Hokkaido Univ 45:42–47

Barr DJ, Ohtsuka S (1989) *Pseudocyclops lepidotus*, a new species of demersal copepod (Calanoida: Pseudocyclopidae) from the Northwestern Pacific. Proc Biol Soc Wash 102:331–338

Barthélémy R, Ohtsuka S, Cuoc C (1998) Description and female genital structures of a new species of the demersal calanoid copepod *Ridgewayia* from southern Japan. J Nat Hist 32:1303–1318

Barthélémy R-M, Ohtsuka S, Soh HY (2003) Mating plug in the planktonic copepod *Tortanus* (*Atortus*). Plankton Biol Ecol 50:25–26

Beltrão R, Monde M, Ueda H (2011) Characteristics and regional classification of the copepod community in Ariake Bay with note on comparison with 3 decades ago. J Oceanogr 67:47–58

Benuys JM (1997) Biomimicry: innovation inspired by nature. Harper Collins, New York

Blades PI, Youngbluth MJ (1979) Mating behavior of *Labidocera aestiva* (Copepoda: Calanoida). Mar Biol 51:339–355

Blanco-Bercial L, Bradford-Grieve J, Bucklin A (2011) Molecular phylogeny of the Calanoida (Crustacea: Copepoda). Mol Phylogenet Evol 59:103–113

Boore JL, Collins TM, Stanton D, Daehler LL, Brown WM (1995) Deducing the pattern of arthropod phylogeny from mitochondrial DNA rearrangements. Nature (Lond) 376:163–165

Böttger-Schnack R (2009) Taxonomy of Oncaeidae (Copepoda Cyclopoida s.l.) from the Red Sea. IX. *Epicalymma bulbosa* sp. nov., first record of the genus in the Red Sea. J Plankton Res 31:1027–1043

Böttger-Schnack R, Machida RJ (2011) Comparison of morphological and molecular traits for species identification and taxonomic grouping of onceaid copepods. Hydrobiologia 666:111–125

Böttger-Schnack R, Schnack D (2013) Definition of species groups of Oncaeidae (Copepoda: Cyclopoida) as basis for a worldwide identification key. J Nat Hist 47:265–288

Boxshall GA, Defaye D (2008) Global diversity of copepods (Crustacea: Copepoda) in freshwater. Hydrobiologia 595:195–207

Boxshall GA, Halsey SH (2004) An introduction to copepod diversity. Ray Society, London

Boxshall GA, Jaume D (2000a) Making waves: the repeated colonization of fresh water by copepod crustaceans. Adv Ecol Res 31:61–79

Boxshall GA, Jaume D (2000b) Discoveries of cave misophrioids (Crustacea: Copepoda) shed light on the origin of anchialine cave faunas. Zool Anz 239:1–19

Bradford-Grieve JM (2002) Colonization of the pelagic realm by calanoid copepods. Hydrobiologia 485:223–244

Bradford-Grieve JM (2004) Deep-sea benthopelagic calanoid copepods and their colonization of the near-bottom environment. Zool Stud 43:276–291

Bradford-Grieve JM, Boxshall GA, Ahyong ST, Ohtsuka S (2010) Cladistic analysis of the calanoid Copepoda. Invertebr Syst 24:291–321

Bradford-Grieve JM, Boxshall GA, Blanco-Bercial L (2014) Revision of basal calanoid copepod families, with a description of a new species and genus of Pseudocyclopidae. Zool J Linn Soc 171:507–533

Brylinski JM, Elvire A, Thomas R, Dorothee V (2012) First record of the Asian copepod *Pseudodiaptomus marinus* Sato, 1913 (Copepoda: Calanoida: Pseudodiaptomidae) in the southern bight of the North Sea along the coast of France. Aquat Invasions 7:577–584

Chae J, Nishida S (1994) Integumental ultrastructure and color pattern in the iridescent copepods of the family Sapphirinidae (Copepoda: Poecilostomatoida). Mar Biol 119:205–210

Chae J, Nishida S (2004) Swimming behaviour and photoresponses of the iridescent copepods, *Sapphirina gastrica* and *Sapphirina opalina* (Copepoda: Poecilostomatoida). J Mar Biol Assoc UK 84:727–731

Chihara M, Murano M (eds) (1997) An illustrated guide to marine plankton in Japan. Tokai University Press, Tokyo (in Japanese)

Cornils A, Blanco-Bercial L (2013) Phylogeny of the Paracalanidae Giesbrecht, 1888 (Crustacea: Copepoda: Calanoida). Mol Phylogenet Evol 69:861–872

Cornils A, Wend-Heckmann B (2015) First report of the planktonic copepod *Oithona davisae* in the northern Wadden Sea (North Sea): evidence for recent invasion? Helgol Mar Res 69:243–248

Dojiri M, Ho J-S (2013) Systematics of the Caligidae, copepods parasitic on marine fishes. Crustac Monogr 19:1–448

Figueroa DF (2011) Phylogenetic analysis of *Ridgewayia* (Copepoda: Calanoida) from the Galapagos and of a new species from the Florida Keys with a reevaluation of the phylogeny of Calanoida. J Crustac Biol 31:153–165

Fleminger A (1973) Pattern, number, variability, and taxonomic significance of integumental organs (sensilla and glandular pores) in the genus *Eucalanus* (Copepoda, Calanoida). Fish Bull 71:965–1010

Fleminger A (1983) Description and phylogeny of *Isascsicalanus paucisetus*, gen. nov., sp. nov. (Copepoda: Calanoida: Spinocalanidae) from an east Pacific hydrothermal vent site (21°N). Proc Biol Soc Wash 96:605–622

Fleminger A (1986) The Pleistocene equatorial barrier between the Indian and Pacific Oceans and a likely cause for Wallace's Line. UNESCO Tech Pap Mar Sci 49:84–97

Fleminger A, Kramer SH (1988) Recent introduction of an Asian estuarine copepod, *Pseudodiaptomus marinus* (Copepoda: Calanoida), into southern California embayments. Mar Biol 98:535–541

Fosshagen A, Iliffe TM (1988) A new genus of Platycopioida (Copepoda) from a marine cave on Bermuda. Hydrobiologia 167(168):357–361

Fosshagen A, Iliffee TM (1985) Two new genera of Calanoida and a new order of Copepoda, Platycopioida, from marine caves on Bermuda. Sarsia 70:345–358

Freeman MA, Anshary H, Ogawa K (2013) Multiple gene analyses of caligid copepods indicate that the reduction of a thoracic appendage in *Pseudocaligus* represents convergent evolution. Parasites Vectors 6:336

Geotze E (2003) Cryptic speciation on the high seas; global phylogenetics of the copepod family Eucalanidae. Proc R Soc Lond B 270:2321–2331

Geotze E, Ohman MD (2010) Integrated molecular and morphological biogeography of the Calanoid copepod family Eucalanidae. Deep-Sea Res II 57:2110–2129

Grice GD, Hulsemann K (1970) New species of bottom-living calanoid copepods collected in deepwater by the DSRV Alvin. Bull Mus Comp Zool 139:185–227

Grygier MJ, Ohtsuka S (2008) A new genus of monstrilloid copepods (Crustacea) with anteriorly pointing ovigerous spines and related adaptations for subthoracic brooding. Zool J Linn Soc 152:459–506

Harada E, Nishino M, Narita T (1985) A partite plankton sampler and summer vertical structure of zooplankton revealed using it in shallow brackish waters, Lake Shinji-ko and Lake Naka-umi. Physiol Ecol Jpn 22:37–57

Harris VA, Iwasaki N (2009) Two new species of *Kensakia* belonging to the family Porcellidiidae (Crustacea, Copepoda, Harpacticoida) from Japan and Malaysia. Bull Natl Mus Nat Sci Ser A Zool 35:157–165

Hattori H (1991) Vertical distribution of zooplankton in the warm core off Sanriku (86B) and adjacent Oyashio water, with special reference to copepods record. Bull Hokkaido Natl Fish Res Inst 55:59–77 (in Japanese with English abstract)

Herring PJ (1988) Copepod luminescence. Hydrobiologia 167(168):183–195

Herring PJ (2007) Sex with the lights on? A review of bioluminescent sexual dimorphism in the sea. J Mar Biol Assoc UK 87:829–842

Herring PJ, Latz MI, Bannister NJ, Widder EA (1993) Bioluminescence of the poecilostomatoid copepod *Oncaea conifera*. Mar Ecol Prog Ser 94:297–309

Hibino M, Ueda H, Tanaka M (1999) Feeding habits of Japanese temperate bass and copepod community in the Chikugo River Estuary, Ariake Sea, Japan. Nippon Suisan Gakkaishi 65:1062–1068 (in Japanese with English abstract)

Hirabayashi T, Ohtsuka S (2014) A new species of *Labidocera* (Copepoda, Calanoida, Pontellidae) collected from Okinawa, southwestern Japan, with establishment of five Indo-West Pacific species groups in the *L. detruncata* species complex. ZooKeys 447:21–34

Hirai J, Shimode S, Tsuda A (2013) Evaluation of ITS2-28S as a molecular marker for identification of calanoid copepods in the subtropical western North Pacific. J Plankton Res 35:644–656

Hirai J, Kuriyama M, Ichikawa T, Hidaka K, Tsuda A (2015) A metagenetic approach for revealing community structure of marine planktonic copepods. Mol Ecol Resour 15:68–80

Hirakawa K, Imamura A, Ikeda T (1992) Seasonal variability in abundance and composition of zooplankton in Toyama Bay, southern Japan Sea. Bull Jpn Sea Fish Res Inst 42:1–15

Hirakawa K, Sakami T, Abo K, Takayanagi K, Tanimura A (2006) Seasonal succession of plankton community structure in fish and pearl oyster farms of Gokasho Bay, Mie Prefecture, Japan. Bull Fish Res Agency 17:37–55 (in Japanese with English abstract)

Hiromi J (1981) Three species of paracalanid copepods in the neighbouring waters of Japan. Bull Plankton Soc Jpn 28:153–164 (in Japanese with English abstract)

Hiromi J (1987) Present knowledge and problems of taxonomy of the family Paracalanidae. Bull Coll Agric Vet Med Nihon Univ 44:147–159 (in Japanese with English abstract)

Hiromi J, Ueda H (1987) Planktonic calanoid copepod *Sinocalanus sinensis* (Centropagidae) from estuaries of Ariake-kai, Japan, with a preliminary note on the mode of introduction from China. Proc Jap Soc Syst Zool 35:19–26

Hirota R (1962) Species composition and seasonal changes of copepod fauna in the vicinity of Mukaishima. J Oceanogr Soc Jpn 18:35–40

Hirota R (1975) Zooplankton investigations in Yatsushirokai, western Kyushu, I. Regional and seasonal occurrences of the important zooplankton. J Oceanogr Soc Jpn 31:115–123

Hirota R (1979) Seasonal occurrence of zooplankton at a definite station off Mukaishima from July of 1976 to June of 1977. Publ Amakusa Mar Biol Lab 5:9–17

Hirota R (1990) Microdistribution of the marine copepod *Oithona davisae* in the shallow waters of Ariake-kai mud flats, Japan. Mar Biol 105:307–312

Hirota R, Hara M (1975) Zooplankton investigations in Yatsushiro-kai, western Kyushu. I. J Oceanogr Soc Jpn 31:115–123

Ho J-S (1990) Phylogenetic analysis of copepod orders. J Crustac Biol 10:528–536

Ho J-S (1994a) Copepod phylogeny: a reconsideration of Huys & Boxshall's 'parsimony versus homology'. Hydrobiologia 292(293):31–39

Ho J-S (1994b) Origin and evolution of the parasitic cyclopoid copepods. Int J Parasitol 24:1293–1300

Ho J-S (2001) Why do symbiotic copepods matter? Hydrobiologia 156:1–7

Ho J-S, Lin C-L (2004) Sea lice of Taiwan. Sueichan Press, Keelung

Ho J-S, Perkins PS (1985) Symbionts of marine Copepoda: an overview. Bull Mar Sci 37:586–598

Ho J-S, Zhang G-X (1994) *Ostrincola koe* (Copepoda, Myicolidae) and mass mortality of cultured hard clam (*Meretrix meretrix*) in China. Hydrobiologia 284:169–173

Ho J-S, G´omez S, Ogawa K, Aritaki M (2004) Two species of parasitic copepods (Caligidae) new to Japan. Syst Parasitol 57:19–34

Ho J-S, Ohtsuka S, Nakadachi N (2006) A new family of poecilostomatoid copepod (Umazuracolidae) based on specimens parasitic on the black scraper (*Thamnaconus modestus*) in Japan. Zool Sci 23:483–496

Hulsemann K (1994) *Calanus sinicus* Brodsky and *C. jashnovi*, nom. nov. (Copepoda: Calanoida) of the north-western Pacific Ocean: a comparison, with notes on the integumental pore pattern in *Calanus* s. str. Invertebr Syst 8:1461–1482

Huys R, Boxshall GA (1991) Copepod evolution. Ray Society, London

Huys R, Llewellyn-Hughes J, Olson PD, Nagasawa K (2006) Small subunit rDNA and Bayesian inference reveal *Pectenophilus ornatus* (Copepoda incertae sedis) as highly transformed Mytilicolidae, and support assignment of Chondracanthidae and Xarifiidae to Lichomolgoidea (Cyclopoida). Biol J Linn Soc 87:403–425

Huys R, Llewellyn-Hughes J, Conroy-Dalton S, Olson PD, Spinks JN, David A, Johnston DA (2007) Extraordinary host switching in siphonostomatoid copepods and the demise of the

Monstrilloida: integrating molecular data, ontogeny and antennulary morphology. Mol Phylogenet Evol 43:368–378

Huys R, Faitih F, Ohtsuka S, Llewellyn-Hughes J (2012) Evolution of the bomolochiform superfamily complex (Copepoda: Cyclopoida): new insights from ssrDNA and morphology, and origin of umazuracolids from polychaete-infesting ancestors rejected. Int J Parasitol 42:71–92

Ianora A, Mazzochi MG, Scotto di Carlo B (1987) Impact of parasitism and intersexuality on Mediterranean populations of *Paracalanus parvus* (Copepoda: Calanoida). Dis Aquat Org 3:29–36

Ishida T (2002) Illustrated fauna of the freshwater cyclopoid copepods of Japan. Bull Biogeogr Soc Jpn 57:37–106 (in Japanese with English abstract)

Ishida T, Kikuchi Y (2000) Illustrated fauna of the freshwater harpacticoid copepods of Japan. Bull Biogeogr Soc Jpn 55:7–94 (in Japanese with English abstract)

Ismail N, Ohtsuka S, Venmathi Maran BA, Tasumi S, Zaleha K, Yamashita H (2013) Complete life cycle of a pennellid *Peniculus minuticaudae* Shiino, 1956 (Copepoda: Siphonostomatoida) infecting cultured threadsail filefish, *Stephanolepis cirrhifer*. Parasite 20:42. doi:10.1051/parasite/2013041

Itoh K (1970) A consideration on feeding habits of planktonic copepods in relation to the structure of their oral parts. Bull Plankton Soc Jpn 17:1–10 (in Japanese with English abstract)

Itoh H (1997) Oncaeidae. In: Chihara M, Murano M (eds) An illustrated guide to marine plankton in Japan. Tokai University Press, Tokyo, pp 978–988

Itoh H (2006) Parasitic and commensal copepods occurring as planktonic organisms with special reference to *Saphirella*-like copepods. Bull Plankton Soc Jpn 53:53–63 (in Japanese with English abstract)

Itoh H, Iizuka S (1979) Studies on the zooplankton in Omura Bay. I. Seasonal occurrence of copepods. Bull Fac Fish Nagasaki Univ 47:5–14 (in Japanese with English abstract)

Itoh H, Nishida S (1991) Occurrence of *Saphirella*-like copepods in Tokyo Bay. In: Uye S-I, NIshida S, Ho J-S (eds) Proceedings of the fourth international conference on Copepoda, Karuizawa, Japan, 16–20 Septermber 1990 (Bulletin of Plankton Society of Japan, Special Volume). Plankton Society of Japan, Higashi, pp 397–403

Itoh H, Nishida S (1995) Copepodid stages of *Hemicyclops japonicus* Itoh and Nishida (Poecilostomatoida: Clausidiidae) reared in the laboratory. J Crustac Biol 15:134–155

Itoh H, Nishida S (2007) Life history of the copepod *Hemicyclops gomsoensis* (Poecilostomatoida, Clausidiidae) associated with decapod burrows in the Tama-River estuary, central Japan. Plankton Benthos Res 2:134–146

Itoh H, Nishida S (2008) Life history of the copepod *Hemicyclops spinulosus* (Poecilostomatoida, Clausidiidae) associated with crab burrows with notes on male polymorphism and precopulatory mate guarding. Plankton Benthos Res 3:189–201

Itoh H, Nishida S (2013) Burrow association of *Hemicyclops* (Copepoda: Poecilostomatoida) as a possible strategy for predator avoidance. Plankton Benthos Res 8:141–149

Itoh H, Nishida S (2015) Spaciotemporal distribution of planktonic copepod communities in Tokyo Bay where *Oithona davisae* Ferrai and Orsi dominated in mid-1980s. J Nat Hist 49:45–48

Itoh H, Ohtsuka S, Sato T (2001) New species of *Tortanus* (Copepoda; Calanoida) from stomach contents of chum salmon juveniles. Plankton Biol Ecol 48:59–67

Itoh H, Mizushima T, Kubota T (2005) Seasonal occurrence of the calanoid copepods from off Miho Key, Suruga Bay, central Honshu, Japan. J Sch Mar Sci Tech Tokai Univ 3:19–32 (in Japanese with English abstract)

Itoh H, Tachibana A, Nomura H, Tanaka Y, Furota T, Ishimaru T (2011) Vertical distribution of planktonic copepods in Tokyo Bay in summer. Plankton Benthos Res 6:129–134

Itoh H, Nakata K, Sasaki K, Ichikawa T, Hidaka K (2014) Seasonal and diel changes in the vertical distribution of oncaeid copepods in the epipelagic zone of the Kuroshio Extension region. Plankton Benthos Res 9:1–14

Ivanenko VN, Defaye D, Cuoc C (2007) A new calanoid copepod (Spinocalanidae) swarming at a cold seep site on the Gabon continental margin (Southeast Atlantic). Cah Biol Mar 48:37–54

Izawa K (1996) *Archidactylina myxinicola*, new genus, new species (Siphostomatoida), in a new family of Copepoda parasitic on hagfishes (Agnatha: Myxniformes). J Crustac Biol 16:406–417

Izawa K (2011) *Dangoka japonica* nov. gen. nov. sp. and *Eudactylinella alba* Wilson, 1932 (Copepoda, Siphonostomatoida, Eudactylinidae) infesting Japanese elasmobranchs. Crustaceana 87:1269–1277

Johnson SC, Treasurer JW, Bravo S, Nagasawa K, Kabata Z (2004) A review of the impact of parasitic copepods on marine aquaculture. Zool Stud 43:229–243

Kaji T, Venmathi Maran BA, Kondoh Y, Ohtsuka S, Boxshall GA, Tsukagoshi A (2012) The lunule of caligid copepods: an evolutionarily novel structure. Evol Dev 14:465–475

Kang Y-S (1996) Redescription of *Paracalanus parvus* and *P. indicus* (Copepoda: Paracalanidae) recorded in the Korean waters. J Korean Fish Soc 29:409–413 (in Korean with English abstract)

Karanovic T, Grygier MJ, Lee W (2013) Endemism of subterranean *Diacyclops* in Korea and Japan, with descriptions of seven new species of the *languidoides*-group and redescriptions of *D. brevifurcus* Ishida, 2006 and *D. suoensis* Ito, 1954 (Crustacea, Copepoda, Cyclopoida). ZooKeys 267:1–76

Kase T, Hayami I (1992) Unique submarine cave mollusc fauna: composition, origin and adaptation. J Molluscan Stud 58:446–449

Kikuchi Y (1991) Tasunori Itô (1945–1990): an obituary. J Crustac Biol 11:179–182

Kim J, Kim W (2000) Molecular phylogeny of poecilostome copepods based on the 18S rDNA sequences. Korean J Biol Sci 4:257–261

Kim I-H, Sato S (2010) A review of copepods associated with bivalves in Japan, with description of two new species (Crustacea, Copepoda, Cyclopoida). Bull Tohoku Univ Mus 9:1–22

Kimmerer WJ, McKinnon AD (1990) High mortality in a copepod population caused by a parasitic dinoflagellates. Mar Biol 107:449–452

Kimoto K, Nakashima J, Morioka Y (1988) Direct observations of copepod swarm in a small inlet of Kyushu, Japan. Sekai Reg Fish Res Lab 66:41–58

Kiso K (1981) On the feeding habit of 0-group crimson sea bream, *Evynnis japonica*, in Shijiki Bay, Hirado Island. Bull Seikai Reg Fish Res Lab 56:15–26

Kiso K (1982) On the feeding habit of 0-group red sea bream (*Pagrus major*) in Shijiki Bay, Hirado Island. II. The habitat utilization in terms of food resources. Bull Seikai Reg Fish Res Lab 57:31–46

Kitahashi T, Kawamura K, Kojima S, Shimanaga M (2013) Assemblages gradually change from bathyal to hadal depth: a case study on harpacticoid copepods around the Kuril Trench (northwest Pacific Ocean). Deep-Sea Res I 74:39–47

Kitahashi T, Jenkins RG, Nomaki H, Shimanaga M, Fujikura K, Kijima S (2014a) Effect of the 2011 Tohoku Earthquake on deep-sea meiofaunal assemblages inhabiting the landward slope of the Japan Trench. Mar Geol 358:128–137

Kitahashi T, Kawamura K, Kojima S, Shimanaga M (2014b) Bathymetric patterns of α and β diversity of harpacticoid copepods at the genus level around the Ryukyu Trench, and turnover diversity between trenches around Japan. Prog Oceanogr 123:54–63

Kobari T, Ban S (1998) Life cycles of two limnetic cyclopoid copepods, *Cyclops vicinus* and *Thermocyclops crassus,* in two different habitats. J Plankton Res 20:1073–1086

Kobari T, Ikeda T (2001) Ontogenetic vertical migration and life cycle of *Neocalanus plumchrus* (Crustacea: Copepoda) in the Oyashio region, with notes on regional variations in body sizes. J Plankton Res 23:287–302

Koehl MAR, Strickler JR (1981) Copepod feeding currents: food capture at low Reynolds number. Limnol Oceanogr 26:1062–1073

Kuriyama M, Nishida S (2006) Species diversity and niche-partitioning in the pelagic copepods of the family Scolecitrichidae (Calanoida). Crustaceana 79:293–317

Lee CE (1999) Rapid and repeated invasions of fresh water by the copepod *Eurytemora affinis*. Evolution 53:1423–1434

Lenz PH (2012) The biogeography and ecology of myelin in marine copepods. J Plankton Res 34:575–589

Lester RJG, Hayward CJ (2006) Phylum Arthropoda. In: Woo PTK (ed) Fish diseases and disorders, vol 1, 2nd edn, Protozoan and metazoan infections. CAB International, London, pp 466–565

Lian D, Uye S (1996a) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. II. *Acartia omorii*. Mar Biol 125:109–117

Lian D, Uye S (1996b) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. III. *Paracalanus* sp. Mar Biol 127:219–227

Lian D, Uye S, Onbé T (1996) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. I. *Centropages abdominalis*. Mar Biol 124:527–536

Machida RJ, Miya MU, Nishida M, Nishida S (2002) Complete mitochondrial DNA sequence of *Tigriopus japonicus* (Crustacea: Copepoda). Mar Biotechnol 4:406–417

Machida RJ, Miya MU, Nishida M, Nishida S (2006) Molecular phylogeny and evolution of the pelagic copepod genus *Neocalanus* (Crustacea: Copepoda). Mar Biol 148:1071–1079

Makino W, Tanabe AS (2009) Extreme population genetic differentiation and secondary contact in the freshwater copepod *Acanthodiaptomus pacificus* in the Japanese Archipelago. Mol Ecol 18:3699–3713

Markhaseva EL, Schulz K (2008) *Caudacalanus* (Copepoda, Calanoida): a new benthopelagic genus from the abyss of the tropical South Atlanitc and Southern Ocean. Zootaxa 1866:277–289

Matsuura H, Nishida S (2000) Fine structure of the "button setae" in the deep-sea pelagic copepods of the genus *Euaugaptilus* (Calanoida: Augaptilidae). Mar Biol 137:339–345

Matsuura H, Nishida S, Nishikawa J (2010) Species diversity and vertical distribution of the deep-sea copepods of the genus *Euaugaptilus* in the Sulu and Celebes Seas. Deep-Sea Res II 57:2098–2109

Mauchline J (1998) The biology of calanoid copepods. Adv Mar Biol 33:1–710

Miller CB (1988) *Neocalanus flemingeri,* a new species of Calanidae (Copepoda: Calanoida) from the subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* (Marukawa) 1921. Prog Oceanogr 20:223–273

Miller CB, Terazaki M (1989) The life cycle of *Neocalanus flemingeri* and *Neocalanus plumchrus* in the Sea of Japan. Bull Plankton Soc Jpn 36:27–41

Nagasawa K (2004) Sea lice, *Lepeophtheirus salomonis* and *Caligus orientalis* (Copepoda: Caligidae), of wild and farmed fish in sea and brackish waters of Japan and adjacent regions: a review. Zool Stud 43:173–178

Nagasawa K, Besciani J, Lutzen J (1988) Morphology of *Pectenophilus ornatus* new genus, new species, a copepod parasite of the Japanese scallop *Patinopecten yessoensi*s. J Crustac Biol 8:31–42

Nagasawa K, Inoue A, Myat S, Umino T (2007) New host records for *Lernaea cyprinacea* (Copepoda), a parasite of freshwater fishes, with a checklist of the Lernaeidae in Japan (1915–2007). J Grad Sch Biosph Sci Hiroshima Univ 46:21–33

Nagasawa J, Uyeno D, Tang D (2010) A checklist of copepods of the genus *Caligus* (Siphonostomatoida, Caligidae) from fishes in Japanese waters (1927–2010). Bull Biogeogr Soc Jpn 65:103–122 (in Japanese with English abstract)

Neibar MT, Hartke TR, Stemme T, Bergmann A, Rust J, Iliffe TM, Koenemann S (2011) Global biodiversity and phylogenetic evaluation of Remipedia (Crustacea). PLoS One 6:e19627

Nishibe Y, Hirota Y, Ueda H (2009) Community structure and vertical distribution of oncaeid copepods in Tosa Bay, southern Japan. J Mar Biol Assoc UK 89:491–498

Nishibe Y, Takahashi K, Ichikawa T, Hidaka K, Kurogi H, Segawa K, Saito H (2015) Degradation of discarded appendicularian houses by oncaeid copepods. Limnol Oceanogr 60:967–976

Nishida S (1985) Pelagic copepods from Kabira Bay, Ishigaki Island, southwestern Japan, with the description of a new species of the genus *Pseudodiaptomus*. Publ Seto Mar Biol Lab 30:125–144

Nishida S (1986) Structure and function of the cephalosome-flap organ in the family Oithonodae (Copepoda, Cyclopoida). Syllogeus 58:385–391

Nishida S, Ferrari FD (1983) Redescription of *Oithona brevicornis* Giesbrecht and *O. aruensis* Früchtl, new rank, with notes on the status of *O. spinulosa* Lindberg. Bull Plankton Soc Jpn 30:71–80

Nishida S, Ohtsuka S (1996) Specialized feeding mechanism in the pelagic copepod genus *Heterorhabdus* (Calanoida: Heterorhabdidae), with special reference to the mandibular tooth and labral glands. Mar Biol 126:619–632

Nishida S, Ohtsuka S (1997) Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecitrichidae. Plankton Biol Ecol 44:81–90

Nishida S, Tanaka O, Omori M (1977) Cyclopoid copepods of the family Oithonidae in Suruga Bay and adjacent waters. Bull Plankton Soc Jpn 24:120–157

Nishida S, Oh B, Nemoto T (1991) Midgut structure and food habits of the mesopelagic copepods *Lophothrix frontalis* and *Scottocalanus securifrons*. In: Uye S-I, Nishida S, Ho J-S (eds) Proceedings of the Fourth International Conference on Copepoda, Karuizawa, Japan, 16–-20 September 1990 (Bulletin of Plankton Society of Japan, Special Volume). Plankton Society of Japan, Higashi, pp 527–534

Nishida S, Kikuchi T, Toda T (1999) Efficient capture of deep-sea hyperbenthic calanoid copepods with baited traps. Plankton Biol Ecol 46:165–168

Nishida S, Ohtsuka S, Parker AR (2002) Functional morphology and food habits of deep-sea copepods of the genus *Cephalophanes* (Calanoida: Phaennidae): perception of bioluminescence as a strategy for food detection. Mar Ecol Prog Ser 227:157–171

Nishimura S (1981) Chikyū no umi to seimei: kaiyou seibutsu chirigaku josetsu [Ocean and life on Earth: marine biogeography introduction]. Kaimeisha, Tokyo (in Japanese)

Nonomura T, Machida RJ, Nishida S (2008) Stage-V copepodites of *Calanus sinicus* and *Calanus jashnovi* (Copepoda: Calanoida) in mesopelagic zone of Sagami Bay as identified with genetic markers, with special reference to their vertical distribution. Prog Oceanogr 77:45–55

Ogawa K (1996) Diseases caused by parasites. In: Muroga K, Egusa S (eds) Introduction to fish pathology. Kouseikaku-Koseisha, Tokyo, pp 95–108 (in Japanese)

Oh B-C, Terazaki M, Nemoto T (1991) Some aspects of the life history of the subarctic copepod *Neocalanus cristatus* (Calanoida) in Sagami Bay, central Japan. Mar Biol 111:207–212

Ohtsuka S (1984) Calanoid copepods collected from the near-bottom in Tanabe Bay on the Pacific coast of the Middle Honshu, Japan. I. Arietellidae. Publ Seto Mar Biol Lab 29:359–365

Ohtsuka S (1985) Calanoid copepods collected from the near-bottom in Tanabe Bay on the Pacific coast of the Middle Honshu, Japan. II. Arietellidae (cont.). Publ Seto Mar Biol Lab 30:287–306

Ohtsuka S (1992) Calanoid copepods collected from the near-bottom in Tanabe Bay on the Pacific coast of the Middle Honshu, Japan. IV. Pseudocyclopiidae. Publ Seto Mar Biol Lab 35:295–301

Ohtsuka S (1999) Evolution of copepods: pattern and process. Aquabiology 21:463–470 (in Japanese with English abstract)

Ohtsuka S (2010) Diversity of parasitic copepods with a special reference to sea lice. Jpn J Vet Parasitol 9:1–8 (in Japanese)

Ohtsuka S, Boxshall GA (1994) *Platycopia orientalis*, new species (Copepoda: Platycopioida), from the North Pacific, with descriptions of copepodid stages. J Crustac Biol 14:151–167

Ohtsuka S, Boxshall GA (2004) A new species of the deep-sea copepod genus *Scutogerulus* (Calanoida: Arietellidae) from the hyperbenthic waters of Okinawa, Japan. Syst Biodivers 2:49–55

Ohtsuka S, Hiromi J (1987) Calanoid copepods collected from the near-bottom in Tanabe Bay on the Pacific coast of the Middle Honshu, Japan. III. Stephidae. Publ Seto Mar Biol Lab 32:219–232

Ohtsuka S, Hiromi J (2009) Tiny invasive aliens: Copepoda. In: The Plankton Society of Japan and The Japanese Association of Benthology (ed) Marine aliens introduced by human activities and their impacts on ecosystems and industries. Tokai University Press, Tokyo, pp 123–134 (in Japanese)

Ohtsuka S, Huys R (2001) Sexual dimorphism in calanoid copepods: morphology and function. Hydrobiologia 453(454):441–466

Ohtsuka S, Kimoto K (1989) *Tortanus* (*Atorus*) (Copepoda: Calanoida) of southern Japanese waters, with descriptions of two new species, *T.* (*A.*) *digitalis* and *T.* (*A.*) *ryukyuensis*, and discussion on distribution and swarming behavior of *Atortus*. J Crustac Biol 9:392–408

Ohtsuka S, Kubo N (1991) Larvaceans and their houses as important food for some pelagic copepods. In: Uye S-I, NIshida S, Ho J-S (eds) Proceedings of the Fourth International Conference on Copepoda, Karuizawa, Japan, 16–20 Septermber 1990, Bulletin of Plankton Society of Japan, special volume. Plankton Society of Japan, Higashi, pp 535–551

Ohtsuka S, Nishida S (1997) Reconsideration on feeding habits of marine pelagic copepods (Crustacea). Umi no Kenkyū 6:299–320 (in Japanese with English abstract)

Ohtsuka S, Onbé T (1989) Evidence of selective feeding on larvaceans by the pelagic copepod *Candacia bipinnata* (Calanoida: Candaciidae). J Plankton Res 11:869–872

Ohtsuka S, Onbé T (1991) Relationship between mouthpart structures and in situ feeding habits of species of the family Pontellidae (Copepoda: Calanoida). Mar Biol 111:213–225

Ohtsuka S, Reid JW (1998) Phylogeny and zoogeography of the planktonic genus *Tortanus* (Calanoida: Tortanidae), with establishment of a new subgenus and descriptions of two new species. J Crustac Biol 18:774–807

Ohtsuka S, Ueda H (1999) Zoogeography of pelagic copepods in Japan and its adjacent waters. Bull Plankton Soc Jpn 46:1–20 (in Japanese with English abstract)

Ohtsuka S, Fukuura Y, Go A (1987) Description of a new species of *Tortanus* (Copepoda: Calanoida) from Kuchinoerabu Island, Kyushu, with notes on its possible feeding mechanism and in-situ feeding habits. Bull Plankton Soc Jpn 34:53–63

Ohtsuka S, Fosshagen A, Go A (1991) The hyperbenthic calanoid copepod *Paramisophria* from Okinawa, south Japan. Zool Sci 8:793–804

Ohtsuka S, Huys R, Boxshall GA, Itô T (1992) *Misophriopsis okinawensis* sp. nov. (Crustacea: Copepoda) from hyperbenthic waters off Okinawa, South Japan, with definitions of related genera *Misophria* Boeck, 1864 and *Stygomisophria* gen. nov. Zool Sci 9:859–874

Ohtsuka S, Kubo N, Okada M, Gushima K (1993) Attachment and feeding of pelagic copepods on larvacean houses. J Oceanogr 49:115–120

Ohtsuka S, Ueda H, Lian G-S (1995) *Tortanus derjugini* Smirnov (Copepoda: Calanoida) from the Ariake Sea, western Japan, with notes on the zoogeography of brackish water calanoid copepods in East Asia. Bull Plankton Soc Jpn 42:147–162

Ohtsuka S, Böttger-Schnack R, Okada M, Onbé T (1996a) In situ feeding habits of *Oncaea* (Copepoda: Poecilostomatoida) from the upper 250 m of the central Red Sea, with special reference to consumption of appendicularian houses. Bull Plankton Soc Jpn 43:89–105

Ohtsuka S, Fosshagen A, Soh HY (1996b) Three new species of the demersal calanoid copepod *Placocalanus* (Ridgewayiidae) from Okinawa, southern Japan. Sarsia 81:247–263

Ohtsuka S, Soh HY, Nishida S (1997) Evolutionary switching from suspension feeding to carnivory in the calanoid family Heterorhabdidae (Copepoda). J Crustac Biol 17:577–595

Ohtsuka S, Soh HY, Ueda H (1998) *Platycopia compacta* sp. n., the second species of Platycopioida (Crustacea: Copepoda) in the Indo-Pacific Region, with remarks on development, feeding, and zoogeography. Zool Sci 15:415–424

Ohtsuka S, Hoshina T, Seike Y, Ohtani S, Kunii H (1999) Seasonal changes of zooplankton community in Honjyo area and its neighboring waters of Lake Naka-umi. Laguna 6:73–87 (in Japanese with English abstract)

Ohtsuka S, Boxshall GA, Torigoe K (2000a) A new genus and species of the family Mantridae (Copepoda: Cyclopoida) infesting the bivalve *Pseudochama retroversa* from the Seto Inland Sea, western Japan. J Nat Hist 34:1967–1976

Ohtsuka S, El-Sherbiny MM, Ueda H (2000b) Taxonomy, functional morphology, and behavioral ecology of the planktonic copepod *Tortanus* (*Atortus*). Crustac Res 29:1–11

Ohtsuka S, Nagasawa K, Gejima K (2000c) Review of parasites of marine zooplankton. Bull Plankton Soc Jpn 47:1–16 (in Japanese with English abstract)

Ohtsuka S, Nishida S, Nakaguchi K (2002) Three new species of the genus *Macandrewella* (Copepoda: Calanoida: Scolecitrichidae) from the Pacific Ocean, with notes on distribution and feeding habits. J Nat Hist 36:531–564

Ohtsuka S, Boxshall GA, Fosshagen A (2003) A new species of *Neoscolecithrix* (Crustacea; Copepoda; Calanoida) from off Okinawa, southwestern Japan, with comments on the generic position in the superfamily Clausocalanoidea. Bull Natl Sci Mus Tokyo Ser A 29:53–63

Ohtsuka S, Ho J-S, Nagasawa K (2004a) Ergasilid copepods (Poecilostomatoida) in plankton samples from Hokkaido, Japan, with reconsideration of the taxonomic status of *Limnoncaea* Kokubo, 1914. J Nat Hist 38:471–498

Ohtsuka S, Ho J-S, Nagasawa K, Morozinska-Gogol J, Piasecki W (2004b) The identity of *Limnoncaea diuncata* Kokubo, 1914 (Copepoda: Poecilostomatoida) from Hokkaido, Japan, with the relegation of *Diergasilus* Do, 1981 to a junior synonym of *Thersitina* Norman, 1905. Syst Parasitol 57:35–44

Ohtsuka S, Hora M, Suzaki T, Arikawa M, Omura G, Yamada Y (2004c) Morphology and host-specificity of the apostome ciliate *Vampyrophrya pelagica* infecting pelagic copepods in the Seto Inland Sea, Japan. Mar Ecol Prog Ser 282:129–142

Ohtsuka S, Horiguchi T, Lopes RM, Choi K-H, Iwasaki K (2004d) Plankton introduction via ballast water: a review. Bull Plankton Soc Jpn 51:101–118 (in Japanese with English abstract)

Ohtsuka S, Boxshall GA, Harada S (2005a) A new genus and species of nicothoid copepod (Crustacea: Copepoda: Siphonostomatoida) parasitic on the mysid *Siriella okadai* Ii from off Japan. Syst Parasitol 62:65–81

Ohtsuka S, Boxshall GA, Shimomura M (2005b) Three new species of deep-sea hyperbenthic Aetideid copepods (Crustacea) collected from Nansei Islands, southwestern Japan. In: Hasegawa K, Shinohara G, Takeda M (eds) Deep-sea fauna and pollutants in Nansei Islands, vol 29, National science museum monographs. National Science Museum, Tokyo, pp 224–247

Ohtsuka S, Itoh G, Mizushima T (2005c) A new species of the calanoid copepod genus *Centropages* (Crustacea) collected from Shimizu Port, Middle Japan: introduced or not? Plankton Biol Ecol 52:92–99

Ohtsuka S, Harada S, Shimomura M, Boxshall GA, Yoshizaki R, Ueno D, Nitta Y, Iwasaki S, Okawachi H, Sakakihara T (2007a) Temporal partitioning: dynamics of alternating occupancy of a host microhabitat by two different crustacean parasites. Mar Ecol Prog Ser 348:261–272

Ohtsuka S, Ueda H, Iwabuchi M, Itoh H, Soh HY, Sakaguchi S, Hirano K, Kimura T, Ueno D (2007b) Alien or native to Japan? whether has planktonic copepods recently described from Shimizu Port as a new species been introduced? Bull Plankton Soc Jpn 54:30–38 (in Japanese with English abstract)

Ohtsuka S, Otani M, Soh HY, Kim M, Lee W, Huang C, Kimmerer WJ, Shimono T, Hanyuda T, Kaiwai H, Ueda H, Yamaguchi A (2008) Relationships between presence or absence of non-indigenous copepods and ballast water at some international ports in Japan. Bull Plankton Soc Jpn 55:115–126 (in Japanese with English abstract)

Ohtsuka S, Takami I, Venmathi Maran BA, Ogawa K, Shimono T, Fujita Y, Asakawa M, Boxshall GA (2009a) Developmental stages and growth of *Pseudocaligus fugu* Yamaguti, 1936 (Copepoda: Siphonostomatoida: Caligidae) host-specific to puffer. J Nat Hist 43:1779–1804

Ohtsuka S, Tanimura A, Machida RJ, Nishida S (2009b) Bipolar and antitropical distributions of planktonic copepods. Fossils 85:6–13 (in Japanese with English abstract)

Ohtsuka S, Kitazawa K, Boxshall GA (2010) A new genus of endoparasitic copepods (Cyclopoida: Enterognathidae), forming a gall in the calyx of deep-sea crinoids. Zool Sci 27:689–696

Ohtsuka S, Horiguchi T, Hanamura Y, Yamaguchi A, Shimomura M, Suzaki T, Ishiguro K, Hanaoka H, Yamada K, Ohtani S (2011a) Symbiosis of planktonic copepods and mysids with epibionts and parasites in the North Pacific: diversity and interactions. Crustac Monogr 15:1–14

Ohtsuka S, Huang C, Shen X, Kimmerer W, Soh HY (2011b) Introduction and establishment of zooplankters by ballast water. J Water Waste 53:811–815 (in Japanese)

Ohtsuka S, Shimomura M, Kitazawa K (2012) A new species of *Enterognathus* (Copepoda, Cyclopoida, Enterognathidae) collected from the Seto Inland Sea, western Japan. ZooKeys 180:1–8

Ohtsuka S, Shimizu N, Sato T, Sato Y (2015) Escape from the atomic bomb: miraculous rediscovery of zinc blocks of the Takamochi Mori's taxonomic monograph on planktonic copepods. Bull Plankton Soc Jpn 62:1–6 (in Japanese with English abstract)

Oka S-I, Saisho T (1994) Occurrence of zooplankton in Sumiyo Bay, Amamioshima Island. Composition and abundance in the estuary and surf zone in winter season. Mem Fac Fish Kagoshima Univ 43:51–59 (in Japanese with English abstract)

Omori M (1967) *Calanus cristatus* and submergence of the Oyashio water. Deep-Sea Res 14:525–532

Omori M (2002) Marine planktology in Japan. Plankton Biol Ecol 49:1–8

Ooishi S (1979) Sueo M. Shiino (1908–1978). Crustaceana 36:173–181

Ooishi S (2006) *Loboixys ryukyuensis* (Crustacea: Copepoda: Cyclopoida: Notodelphyidae), a new genus and species, living in the compound ascidian *Diplosoma virens* at Okinawa, Japan. Proc Biol Soc Wash 119:373–383

Orsi JJ, Ohtsuka S (1999) Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biol Ecol 46:128–131

Paffenhöfer G-A, Strickler JR, Alcaraz M (1982) Suspension-feeding by herbivorous calanoid copepods: a cinematographic study. Mar Biol 67:193–199

Piasecki W, Goodwin AE, Eiras JC, Nowak B (2004) Importance of Copepoda in freshwater aquaculture. Zool Stud 43:193–205

Razouls C, de Bovée F, Kouwenberg J, Desreumaux N (2015) Diversity and geographic distribution of marine planktonic copepods. Available at http://copepodes.obs-banyuls.fr/en. Accessed 10 Apr 2015

Saiz E, Calbet A, Broglio E (2003) Effects of small-scale turbulence on copepods: the case of *Oithona davisae*. Limnol Oceanogr 48:1304–1311

Sakaguchi SO, Ueda H (2010) A new species of *Pseudodiaptomus* (Copepoda: Calanoida) from Japan, with notes on the closely related *P. inopinus* Burckhardt, 1913 from Kyushu Island. Zootaxa 2623:52–68

Sakaguchi SO, Ueda J, Ohtsuka S, Soh HY, Yoon YH (2011) Zoogeography of planktonic brackish-water calanoid copepods in western Japan with comparison with neighboring Korean fauna. Plankton Benthos Res 6:18–25

Sano M, Maki K, Nishibe Y, Nagata T, Nishida S (2013) Feeding habits of mesopelagic copepods in Sagami Bay: insights from integrative analysis. Prog Oceanogr 110:11–26

Sano M, Nishibe Y, Tanaka Y, Nishida S (2015) Temporally sustained dietary niche partitioning in two mesopelagic copepod species and their mouth morphology. Mar Ecol Prog Ser 518:51–67

Sato M (ed) (2000) Ariake-kai no ikimono-tachi: higatakakou no seibutsu-tayousei [Life in Ariake Sea: biodiversity in tidal flats and estuaries]. Kaiyusha, Tokyo (in Japanese)

Shimanaga M, Shirayama Y (2005) Precopulatory mate guarding of interstitial *Phyllopodopsyllus* sp. (Copepoda: Harpacticoida) in Otsuchi Bay, northeastern Japan. Benthos Res 60:39–44

Shimanaga M, Kitazato H, Shirayama Y (2004) Temporal patterns in diversity and species composition of deep-sea benthic copepods in bathyal Sagami Bay, central Japan. Mar Biol 144:1097–1110

Shimanaga M, Nomaki H, Iijima K (2008) Spatial changes in the distributions of deep-sea "Cerviniidae" (Harpacticoida, Copepoda) and their associations with environmental factors in the bathyal zone around Sagami Bay, Japan. Mar Biol 153:493–506

Shimode S, Toda T, Kikuchi T (2006) Spatio-temporal changes in diversity and community structure of planktonic copepods in Sagami Bay, Japan. Mar Biol 148:581–597

Shimomura M, Fujita Y (2009) First record of the thermosbaenacean genus *Halosbaena* from Asia: *H. daitoensis* sp. nov. (Peracarida: Thermosbaenacea: Halosbaenidae) from an anchialine cave of Minamidaito-jima Is., in Okinawa, southern Japan. Zootaxa 1990:55–64

Srinui K, Ohtsuka S, Nishida S (2013) A new species of *Pseudodiaptomus* (Crustacea, Copepoda, Calanoida, Pseudodiaptomidae) from the Prasae River Estuary, Gulf of Thailand. ZooKeys 338:39–54

Steele S, Mulcahy MF (2001) Impact of the copepod *Mytilicola orientalis* on the Pacific oyster *Crassostrea gigas* in Ireland. Dis Aquat Org 47:145–149

Stock JH (1993) Copepoda (Crustacea) associated with commercial and non-commercial Bivalvia in the East Scheldt, The Netherlands. Bijdr Dierk 63:61–64

Suarez-Morales E, Kim I-H, Escanilla BJ (2012) On some caligids (Copepoda: Caligidae) from plankton of a coastal lagoon in the Gulf of Mexico with a description of a new species of *Metacaligus*. Zool Stud 51:804–818

Suzuki H, Matsutani T (2009) Infection of the parasitic copepod, *Pectenophilus ornatus* on juvenile Japanese scallop, *Patinopecten yessoensis*. Aquacult Sci 57:513–514 (in Japanese with English abstract)

Suzuki KW, Kasai A, Isoda T, Nakayama K, Tanaka M (2008) Distinctive stable isotope ratios in important zooplankton species in relation to estuarine salinity gradients: potential tracer of fish migration. Estuar Coast Shelf Sci 78:541–550

Takemori Y, Iwasaki N (2009) A new species of *Thalestris* (Crustacea: Copepoda: arpacticoida: Thalestridae) from Japan, infesting the red alga *Palmaria palmate*. Species Divers 14:285–295

Takenaka Y, Noda-Ogura A, Imanishi T, Yamaguchi A, Gojobori T, Shigeri Y (2013) Computational analysis and functional expression of ancestral copepod luciferase. Gene (Amst) 528:201–205

Tanaka O (1960) The pelagic copepods of the Izu region, Middle Japan. Systematic account VI. Phaennidae and Tharybidae. Publ Seto Mar Biol Lab 8:85–135

Tanaka O (1966) Neritic Copepoda Calanoida from the north-west coast of Kyushu. Proc Symp Crustac I 1:38–50

Tang D, Izawa K (2005) *Biacanthus pleuronichthydis* (Yamaguti, 1939) gen. n., comb. n. (Copepoda: Taeniacanthidae), an ectoparasite of flatfishes from Japanese waters. Zootaxa 1071:47–60

Tang D, Uyeno D, Nagasawa K (2010) Pseudohatschekiidae, a new family for *Pseudohatschekia branchiostegi* Yamaguti, 1939 (Crustacea: Copepoda: Siphonostomatoida) from *Branchiostegus* spp. (Teleostei: Perciformes: Malacanthidae) in Japanese waters, with descriptions of the early developmental stages of *P. branchiostegi*. Syst Parasitol 77:215–231

Tanimura A, Hoshiai T, Fukuchi M (1996) The life cycle strategy of the ice-associated copepod, *Paralabidocera antarctica* (Calanoida, Copepoda), at Syowa Station, Antarctica. Antarct Sci 8:257–266

Tasumi S, Ismail N, Boxshall GA, Kikuchi K, Suzuki Y, Ohtsuka S (2015) Screening of candidate genes encoding proteins expressed in pectral fins of fugu *Takifugu rubripes*, in relation to habitat site of parasitic copepod *Caligus fugu*, using suppression subtractive hybridization. Fish Shellfish Immunol 44:356–364

Temnykh A, Nishdia S (2012) New record of the planktonic copepod *Oithona davisae* Ferrari and Orsi in the Black Sea with notes on the identity of "*Oithona brevicornis*". Aquat Invasions 7:425–431

Tsuda A, Miller CD (1998) Mate-finding behaviour in *Calanus marshallae* Frost. Philos Trans R Soc Lond B 353:713–720

Tsuda A, Saito H, Kasai H (1999) Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. Mar Biol 135:533–544

Tsuda A, Saito H, Kasai H (2001) Life history strategies of subarctic copepods *Neocalanus flemingeri* and *N. plumchrus*, especially concerning lipid accumulation patterns. Plankton Biol Ecol 48:52–58

Tsuda A, Saito H, Kasai H (2004) Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (Copepoda: Calanoida) in the western subarctic Pacific Ocean. Fish Oceanogr 13(Suppl 1):10–20

Tung C-H, Cheng Y-R, Lin C-Y, Ho J-S, Kuo C-H, Su Y-S (2014) A new copepod with transformed body plan and unique phylogenetic position parasitic in the acorn worm *Ptychodera flava*. Biol Bull 226:69–80

Uchima M (1988) Gut content analysis of neritic copepods *Acartia omorii* and *Otihona davisae* by a new method. Mar Ecol Prog Ser 48:93–97

Uchima M, Murano M (1988) Mating behavior of the marine copepod *Oithona davisae*. Mar Biol 99:39–45

Ueda H (1980) Zooplankton investigation in Shijiki Bay. I. Compositions of zooplankton and distribution of copepods from April to August 1975. Bull Seikai Reg Fish Res Lab 54:171–194 (in Japanese with English abstract)

Ueda H (1982) Zooplankton investigation in Shijiki Bay. II. Zooplankton communities from September 1975 to April 1976, with special reference to distributional characteristics of inlet copepods. Bull Seikai Reg Fish Res Lab 58:1–22 (in Japanese with English abstract)

Ueda H (1991) Horizontal distribution of planktonic copepods in inlet waters. In: Uye S-I, NIshida S, Ho J-S (eds) Proceedings of the Fourth International Conference on Copepoda, Karuizawa, Japan, 16–20 Septermber 1990 (Bulletin of Plankton Society of Japan, Special Volume). Plankton Society of Japan, Higashi, pp 143–160

Ueda H (2001) Distributional ecology of planktonic copepods in inlet waters. Mon Kaiyo 27:96–104 (in Japanese)

Ueda H, Bucklin A (2006) *Acartia* (*Odontacartia*) *ohtsukai*, a new brackish-water calanoid copepod from Ariake Bay, Japan, with a redescription of the closely related *A. pacifica* from the Seto Inland Sea. Hydrobiologia 560:77–91

Ueda H, Ishida T (1997) Species composition and description of limnoplanktonic copepods from Okinawa. Plankton Biol Ecol 44:41–54

Ueda H, Nagai H (2009) Three new species of the brackish-water copepod *Halicyclops* (Crustacea, Cyclopoida) from Ariake Bay, Japan. J Nat Hist 43:287–307

Ueda H, Kuwahara M, Tanaka M, Azeta M (1983) Underwater observation on copepod swarms in temperate and subtropical waters. Mar Ecol Prog Ser 11:165–171

Ueda H, Terao A, Tanaka M, Hibino M, Islam Md S (2004) How can river-estuarine planktonic copepod survive river floods? Ecol Res 19:625–632

Ueda H, Yamaguchi A, Saitoh S-I, Sakaguchi SO, Tachihara K (2011) Speciation of two salinity-associated size forms of *Oithona dissimilis* (Copepoda: Cyclopoida) in estuaries. J Nat Hist 45:2069–2079

Uye S (1982) Seasonal cycles in abundance of major holoplankton in the innermost part of Onagawa Bay, Northeast Japan. J Fac Appl Biol Sci Hiroshima Univ 21:1–10

Uye S (1985) Resting egg production as a life history strategy of marine planktonic copepods. Bull Mar Sci 37:440–449

Uye S, Sano K (1995) Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. Mar Ecol Prog Ser 118:121–128

Uye S, Sano K (1998) Seasonal variations in biomass, growth rate and production rate of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. Mar Ecol Prog Ser 163:37–44

Uye S, Aoto I, Onbé T (2002) Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod. J Plankton Res 24:143–153

Uyeno D, Nagasawa K (2012) *Ttetaloia hoshinoi*, a new genus and species of chondracanthid Copepod (Poecilostomatoida) parasitic on triplefins (Actinopterygii: Tripterygiidae) from Japanese waters. Zoosymposia 8:39–48

Venmathi Maran BA, Ohtsuka S (2008) Descriptions of caligiform copepods in plankton samples collected from East Asia: accidental occurrence or a new mode of life cycle? Plankton Benthos Res 3:202–215

Venmathi Maran BA, Moon SY, Oh S-Y, Soh HY, Myoung J-G (2012a) Redescription of two pennellids (Copepoda, Siphonostomatoida) from Korea with a key to species of *Peniculus* von Nordmann, 1832. ZooKeys 243:1–14

Venmathi Maran BA, Ohtsuka S, Jitchum P (2012b) Occurrence of caligid copepods (Crustacea) in plankton samples collected from Japan and Thailand, with the description of a new species. Species Divers 17:87–95

Venmathi Maran BA, Ohtsuka S, Shang X (2012c) Records of adult caligiform copepods (Crustacea: Copepoda: Siphonostomatoida) in marine plankton from East Asia, including descriptions of two new species of *Caligus* (Caligidae). Species Divers 17:201–219

Venmathi Maran BA, Moon SY, Ohtsuka S, Oh S-Y, Soh HY, Myoung J-G, Iglikowska A, Boxshall GA (2013) The caligid life cycle: new evidence from *Lepeophtheirus elegans* reconciles the cycles of *Caligus* and *Lepeophtheirus* (Copepoda: Caligidae). Parasite 20:15

Wakabayashi K, Otake S, Tanaka Y, Nagasawa K (2013) *Choniomyzon inflatus* n. sp. (Crustacea: Copepoda: Nicothoidae) associated with *Ibacus novemdentatus* (Crustacea: Decapoda: Scyllaridae) from Japanese waters. Syst Parasitol 84:157–165

Walter TC, Ohtsuka S, Putchakarn S, Pinkaew K, Chullasorn S (2002) Redescription of two species of *Pseudodiaptomus* from Asia and Australia (Crustacea: Copepoda: Calanoida: Pseudodiaptomidae) with discussion of the female genital structure and zoogeography of Indo-West Pacific species. Proc Biol Soc Wash 115:650–669

Wyngaard GA, Holyńska M, Schulte JA II (2010) Phylogeny of the freshwater copepod *Mesocyclops* (Crustacea: Cyclopidae) based on combined molecular and morphological data, with notes on biogeography. Mol Phylogent Evol 55:753–764

Yager J, Humphreys WF (1996) *Lasionectes exleyi*, sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean, with a key to the world species. Invertebr Taxon 10:171–187

Yagi Y, Kinoshita I, Fujita S, Ueda H, Aoyama D (2009) Comparison of the early life histories of two *Cynoglossus* species in the inner estuary of Ariake Bay, Japan. Ichthyol Res 56:363–371

Yamada Y, Kobiyama A, Ogata T (2012) Seasonal succession of four *Acartia* copepods (Copepoda, Calanoida) in Okkirai Bay, Sanriku, northern Japan. Plankton Benthos Res 7:188–194

Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi MM (2002) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). Deep-Sea Res I 49:1007–1025

Yamazi I (1955) Plankton investigation in inlet waters along the coast of Japan. XVI. The plankton of Tokyo Bay in relation to the water movement. Publ Seto Mar Biol Lab 4:285–309

York JK, McManus GB, Kimmerer WJ, Slaughter AM, Ignoffo TR (2014) Trophic link in the plankton in the low salinity zone of a large temperate estuary: top-down effects of introduced copepods. Estuar Coasts 37:576–588

Chapter 23
Review of the Taxonomy, Diversity, Ecology, and Other Biological Aspects of Order Tanaidacea from Japan and Surrounding Waters

Keiichi Kakui

Abstract The order Tanaidacea is a group of benthic crustaceans, most of which are small, up to a few millimeters long. Tanaidaceans are distributed worldwide, with more than 1200 described species. Following the first taxonomic paper on a Japanese tanaidacean in 1936, many researchers have studied their taxonomy, morphology, reproductive biology, or ecology in the waters around Japan. This chapter presents a brief introduction to tanaidaceans and then reviews what is known of their systematics (taxonomy and phylogeny), biology (including feeding habits, phenology, morphology, reproductive modes, parasites, predators), and ecology in Japan. The chapter ends with a summary and prospects for future research. The general conclusion is that tanaidaceans have been understudied, both globally and within Japan; the 104 nominal species reported from around Japan and the 1200 species reported globally likely represent a fraction of the actual diversity. The phylogeny of tanaidaceans is largely unresolved at all taxonomic levels. Recent, significant new discoveries concerned with herbivory, selfing, skin-digging activity in holothuroid hosts, possible sound production, and tube building suggest that much remains to be learned about their general biology.

Keywords Crustacea • Peracarida • Tanaidacea • Taxonomy • Biology • Ecology • Japan

23.1 Introduction

The order Tanaidacea is a group of aquatic crustaceans in the superorder Peracarida, which includes Isopoda, Amphipoda, Cumacea, and some other groups. More than 1200 living tanaidacean species have been described worldwide, constituting 33 families, with several dozens of species regarded as family *incertae*

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sedis (Anderson 2013); this is likely only a small fraction of the actual species diversity (cf. Błażewicz-Paszkowycz 2014). Tanaidacea also includes a few extinct species; 16 fossil taxa have been recorded from the Lower Carboniferous to the Middle Cretaceous (see Sánchez-García et al. 2015). Tanaidaceans differ from other crustaceans in the following combination of characters: (1) a cephalon and the two most anterior thoracic somites form a cephalothorax, resulting in a pereon consisting of six pereonites; (2) the cephalothorax is covered with a carapace; (3) the cephalothorax has a branchial chamber posterolaterally on each side, each containing an epignath (an organ related to respiration); (4) the appendage on the second thoracic somite (seventh segment in the cephalothorax) is a cheliped (it is subchelate in a few groups; cf. Kakui and Angsupanich 2012); and (5) there is one pair of narrow, biramous, or uniramous uropods.

Tanaidaceans are typically only a few millimeters long, although the largest reported is 75 mm long (Gamo 1984). Although several groups inhabit nonmarine environments such as brackish lakes, freshwater systems, and anchialine caves (Kakui et al. 2010; Chapman et al. 2011; Guţu and Iliffe 2011; Blazewicz-Paszkowycz et al. 2012), most species are marine. Marine species have been reported worldwide, ranging in depth from the intertidal zone to bathyal depths at around 9000 m. Aside from a few parasitic or symbiotic species such as *Exspina typica* and *Terebellatanais floridanus* (Alvaro et al. 2011; Suárez-Morales et al. 2011), tanaidaceans are free living (cf. Błażewicz-Paszkowycz 2014). They show diverse modes of life (Fig. 23.1); for example, most apseudomorph tanaidaceans are burrowers; some species in the family Pagurapseudidae utilize empty gastropod shells as a mobile shelter, resembling hermit crabs; and many species use threads to construct tube-like nests in the sea bottom, or on the surfaces of seaweeds, seagrasses, other animals, or abiotic substrata (Hassack and Holdich 1987; Kakui and Hiruta 2014; hereafter, 'tube-dwellers'). Tanaidaceans are typical peracaridans, in that they lack a planktonic larval stage and brood their young, and release benthic offspring directly (so-called direct development), a feature that might be responsible for the occasionally extremely high local densities reported, for example, 146,000 individuals/m^2 in *Allotanais hirsutus* and

Fig. 23.1 Examples of modes of life among tanaidaceans. (**a**) A sphyrapodid in its burrow. (**b**) A pagurapseudid inhabiting an empty gastropod shell. (**c**) A tanaidid in its self-woven, tube-like nest (*arrow*) on a seagrass leaf (tube-dweller)

140,000 individuals/m^2 in *Mesokalliapseudes crassus* (Barnard 1970; Delille et al. 1985).

The earliest report of tanaidaceans from the waters surrounding Japan was that by Stephensen (1936), reporting a tanaidid species collected in the Kurile Islands. There have been many subsequent studies, continuing to the present, that discuss taxonomy, phylogeny, biology, and ecology. In this chapter, I review previous studies on the systematics, biology, and ecology of tanaidaceans around Japan.

23.2 Systematics

Tanaidacean systematics (including taxonomy) remains active, with recent discoveries of taxa even at the family level (e.g., Larsen 2012). In this section, I review tanaidacean systematics around Japan.

23.2.1 Taxonomic and Phylogenetic Studies of Tanaidaceans Around Japan

Knud Hensch Stephensen, a Danish zoologist, published the first report specifically about a tanaidacean from Japanese waters. This study (Stephensen 1936), based on specimens collected by Denzaburo Miyadi from a lake on Kunashiri Island, Kurile Islands, reported and redescribed *Sinelobus stanfordi*.

The first Japanese specialist on tanaidacean taxonomy was Sueo Shiino, who also actively studied other crustaceans, including isopods, copepods, and rhizocephalans. His publications include five papers on the Japanese tanaidacean fauna (Shiino 1937, 1951a, b, 1952, 1966), with descriptions of seven new species, as well as five papers on tanaidaceans outside Japan (e.g., Shiino 1963).

Another relevant specialist was the Soviet researcher Rosalia Konstantinovna Kudinova-Pasternak, who studied deep-sea tanaidaceans collected from the Sea of Japan, the Kurile–Kamchatka Trench, the Japan Trench, the Izu–Ogasawara Trench, and the Pacific abyssal plain, and described more than 25 new species from these areas (Kudinova-Pasternak 1966a, b, 1970, 1976, 1978, 1984). Other researchers were active around the same time. Kussakin and Tzareva (1972) described several tanaidomorphs from the Kurile Islands. Sieg (1980) described two new tanaidids, *Zeuxo coralensis* and *Z. maledivensis*; although the type locality of these species is the Maldive Islands, Sieg included Japanese specimens in the material examined for the original descriptions. Ishimaru (1985) described two leptocheliids, one of which was new to science.

After a hiatus of nearly two decades in Japanese tanaidacean studies, Nunomura (2005) described a new brackish apseudomorph from Okinawa. A further boost to tanaidacean taxonomy came in 2007, when the Danish researcher Kim Richard Larsen came to Japan for a 2-year stay. He and his host, Michitaka Shimomura, studied both shallow-water and deep-sea tanaidaceans, described 12 new species in four papers, and edited a monograph (with the participation of four other researchers) that included descriptions of 15 new species (Larsen and Shimomura 2006, 2007a, b, 2008, 2009; Bamber 2007; Bird 2007a, b; Błażewicz-Paszkowycz 2007; Larsen 2007; McLelland 2007). Around the same time, my colleagues and I began studies that resulted in 8 new species described from Japan, with several redescriptions (Kakui et al. 2007, 2010, 2012; Kakui and Kajihara 2011; Kakui and Yamasaki 2013; Kakui and Kohtsuka 2015; Kakui and Naruse 2015). Another currently active specialist is the Polish researcher Magdalena Błażewicz-Paszkowycz, who has published descriptions of 9 new species collected by two joint Russian–German expeditions, SoJaBio (Sea of Japan) and KuramBio (Kurile–Kamchatka Trench) (Błażewicz-Paszkowycz et al. 2013, 2015a, b).

The known tanaidacean fauna around Japan currently stands at 104 species (Table 23.1, Fig. 23.2), although some of these records may be in error because of misidentification (Błażewicz-Paszkowycz et al. 2013). Some papers have only presented new distributional records or partial descriptions (e.g., Nunomura 1985; Ariyama and Ohtani 1990; Saito 1996; Kakui et al. 2014).

Since the pioneering work by Drumm (2010), three molecular phylogenetic studies on tanaidaceans have been published, all of which have included representative species collected around Japan. Kakui et al. (2011) focused on the relationships among families or higher taxa and obtained the first sequence data from neotanaids; based on the results, these authors proposed a two-suborder, four-superfamily classification for Recent tanaidaceans. Kakui et al. (2012) and Błażewicz-Paszkowycz et al. (2015b) studied the phylogenetic position of *Arctotanais* and *Protanais*, respectively, within Tanaidomorpha.

23.2.2 Some Remarks on the Tanaidacean Fauna Around Japan

Japan extends across several climatic zones and is affected by two warm and two cold currents, and thus the tanaidacean fauna in coastal area shows some regionality (Kakui, unpublished data from several years of sampling, including by snorkeling and SCUBA). At the family level, for example, Kalliapseudidae, Parapseudidae, Apseudidae, and Pagurapseudidae have been detected only from Honshu to the Nansei Islands, but not around Hokkaido. Metapseudidae from coastal regions includes species in genera previously reported (*Apseudomorpha* and *Synapseudes*; Shiino 1951b) as well as representatives of other genera such as *Curtipleon* (Kakui, unpublished data), with differences in distributional ranges among genera. To date,

Table 23.1 Tanaidacean species recorded around Japan

Classification/species	References[a]
Apseudomorpha	
Apseudoidea	
Apseudidae	
Apseudes nipponicus	Shiino (1937)
Carpoapseudes spinigena	Larsen and Shimomura (2007b)
Carpoapseudes varindex	Larsen and Shimomura (2007b)
Fageapseudes brachyomos	Larsen and Shimomura (2007b)
Paradoxapseudes littoralis	Shiino (1952)
Kalliapseudidae	
Phoxokalliapseudes tomiokaensis	Shiino (1966)
Metapseudidae	
Apseudomorpha albida	Shiino (1951b)
Hoplomachus toyoshious	Larsen and Shimomura (2006)
Synapseudes setoensis	Shiino (1951b)
Pagurapseudidae	
Indoapseudes bamberi	Kakui and Naruse (2015)
Parapseudidae	
Longiflagrum nasutus	Nunomura (2005)
Longipedis fragilis	Larsen and Shimomura (2006)
Parapseudes algicola	Shiino (1952)
Parapseudes arenamans	Larsen and Shimomura (2008)
Sphyrapodidae	
Kudinopasternakia balanorostrata	Kakui and Kajihara (2011)
Pseudosphyrapus cuspidiger	Kakui and Kajihara (2011)
Pseudosphyrapus malyutinae	Błażewicz-Paszkowycz et al. (2013)
Pseudosphyrapus quintolongus	Kakui et al. (2007)
Pseudosphyrapus serratus[b]	Kudinova-Pasternak (1984)
Tanaidomorpha	
Neotanaoidea	
Neotanaidae	
Neotanais americanus	Kudinova-Pasternak (1978)
Neotanais kuroshio	Larsen and Shimomura (2007b)
Neotanais oyashio	Larsen and Shimomura (2007b)
Neotanais tuberculatus	Kudinova-Pasternak (1970)
Neotanais wolffi	Kudinova-Pasternak (1966b)
Paratanaoidea	
Agathotanaidae	
Agathotanais hadalis	Larsen and Shimomura (2007b)
Agathotanais ingolfi[b]	Kudinova-Pasternak (1970)
Agathotanais misakiensis	Kakui and Kohtsuka (2015)
Agathotanais toyoshioae	Kakui and Kohtsuka (2015)

(continued)

Table 23.1 (continued)

Classification/species	References[a]
Paragathotanais abyssorum	Larsen and Shimomura (2007b)
Paranarthrura vitjazi	Larsen and Shimomura (2007b)
Akanthophoreidae	
Akanthophoreus crassicauda	Larsen and Shimomura (2007b)
Akanthophoreus gracilis[b]	Kudinova-Pasternak (1984)
Akanthophoreus imputatus	Larsen and Shimomura (2007b)
Akanthophoreus lispopygmos	Błażewicz-Paszkowycz et al. (2013)
Akanthophoreus longiremis[b]	Kudinova-Pasternak (1978)
Akanthophoreus undulatus	Larsen and Shimomura (2007b)
Akanthophoreus verutus	Błażewicz-Paszkowycz et al. (2013)
Chauliopleona armata[b]	Kudinova-Pasternak (1984)
Chauliopleona hansknechti	Larsen and Shimomura (2007a)
Chauliopleona sinusa	Larsen and Shimomura (2009)
Anarthruridae	
Anarthruropsis langi	Kudinova-Pasternak (1976)
Anarthruropsis longa	Kudinova-Pasternak (1984)
Keska sei	Błażewicz-Paszkowycz et al. (2013)
Siphonolabrum tenebrosus	Larsen and Shimomura (2007b)
Colletteidae	
Collettea cylindrata[b]	Kudinova-Pasternak (1970)
Collettea minima	Kudinova-Pasternak (1978)
Leptognathiopsis langi	Larsen and Shimomura (2007b)
Nippognathiopsis petila	Błażewicz-Paszkowycz et al. (2013)
Tumidochelia knighti	Larsen and Shimomura (2007a)
Cryptocopidae	
Cryptocopoides arcticus[b]	Kudinova-Pasternak (1978)
Cryptocopoides pacificus	Larsen and Shimomura (2007b)
Heterotanoididae	
Heterotanoides ornatus	Kudinova-Pasternak (1976)
Leptocheliidae	
Leptochelia itoi	Ishimaru (1985)
Leptochelia savignyi	Shiino (1951a)
Mesotanais birdi	Larsen and Shimomura (2007a)
Pseudonototanais modestus	Kussakin and Tzareva (1972)
Leptognathiidae	
Biarticulata greveae	Kudinova-Pasternak (1976)
Biarticulata parelegans	Kudinova-Pasternak (1970)
Forcipatia rotundicauda	Larsen and Shimomura (2007b)
Leptognathia aneristus	Larsen and Shimomura (2007b)
Leptognathia bamberi	Larsen and Shimomura (2007a)

(continued)

Table 23.1 (continued)

Classification/species	References[a]
Nototanaidae	
Nesotanais ryukyuensis	Kakui et al. (2010)
Nototanoides ohtsukai	Kakui and Yamasaki (2013)
Paranesotanais longicephalus	Larsen and Shimomura (2008)
Paratanaidae	
Paratanais impressus	Kussakin and Tzareva (1972)
Pseudotanaidae	
Pseudotanais abathagastor	Błażewicz-Paszkowycz et al. (2013)
Pseudotanais affinis[b]	Kudinova-Pasternak (1984)
Pseudotanais intortus	Błażewicz-Paszkowycz et al. (2013)
Pseudotanais nipponicus	Larsen and Shimomura (2007b)
Pseudotanais nordenskioldi	Kudinova-Pasternak (1978)
Pseudotanais soja	Błażewicz-Paszkowycz et al. (2013)
Pseudotanais vitjazi	Kudinova-Pasternak (1970)
Tanaellidae	
Arthrura andriashevi	Kudinova-Pasternak (1966a)
Arthrura longicephala	Kudinova-Pasternak (1978)
Tanaella forcifera[b]	Kudinova-Pasternak (1984)
Tanaella kommritzia	Larsen and Shimomura (2007a)
Tanaopsididae	
Tanaopsis curta	Kudinova-Pasternak (1984)
Tanaopsis rugaris	Błażewicz-Paszkowycz et al. (2013)
Typhlotanaidae	
Larsenotanais kamchatikus	Larsen and Shimomura (2007b)
Paratyphlotanais japonicus	Błażewicz-Paszkowycz et al. (2013)
Peraeospinosus magnificus	Larsen and Shimomura (2007b)
Torquella angularis	Larsen and Shimomura (2007b)
Torquella elegans	Kudinova-Pasternak (1978)
Torquella grandis	Kudinova-Pasternak (1970)
Typhlamia mucronata	Kudinova-Pasternak (1970)
Typhlotanais compactus	Larsen and Shimomura (2007b)
Typhlotanais kussakini	Kudinova-Pasternak (1970)
Typhlotanais longicephala	Kudinova-Pasternak (1970)
Typhlotanais magdalensis	Larsen and Shimomura (2007a)
Typhlotanais ohtsukae	Larsen and Shimomura (2007a)
Typhlotanais rectus	Kudinova-Pasternak (1978)
Typhlotanais simplex	Błażewicz-Paszkowycz et al. (2013)
Family incertae sedis	
Leptognathia microcephala	Larsen and Shimomura (2007b)
Leptognathia vinogradovae	Kudinova-Pasternak (1970)
Metatanais cylindricus	Shiino (1952)
Robustochelia robusta	Kudinova-Pasternak (1978)

(continued)

Table 23.1 (continued)

Classification/species	References[a]
Tanaidoidea	
Tanaididae	
Arctotanais alascensis	Kakui et al. (2012)
Protanais birsteini	Błażewicz-Paszkowycz et al. (2015b)
Sinelobus stanfordi	Ariyama and Ohtani (1990)
Tanais tinhauae	Kakui et al. (2011)
Tanais vanis[b]	Sieg (1980)
Zeuxo coralensis	Sieg (1980)
Zeuxo maledivensis	Sieg (1980)
Zeuxo normani	Shiino (1951a)

[a] Only a selected source is presented

[b] The distribution around Japan is questionable

Apseudomorpha has been collected from Hokkaido to the Ryukyu Islands; *Synapseudes* from central Honshu to the Ryukyu Islands; and *Curtipleon* only in the vicinity of the Ogasawara and Ryukyu Islands (Kakui, unpublished data). Nototanaidae is presently known from only around the Ryukyu Islands (Kakui and Yamasaki 2013). These distributional differences may result from differences in habitat preference (e.g., brown alga bed, mudflat, coral reef, etc.) as well as differences in tolerance across a wide range of water temperature related to latitude and ocean currents. In addition, mangrove forests extend farther north in Japan than anywhere else in the world except Bermuda (Giri et al. 2011), contributing to tanaidacean diversity; as evidenced, for example, by the nototanaid *Nesotanais ryukyuensis*, so far known only from brackish waters around islands with mangroves (Kakui and Yamasaki 2013). Similarly, the parapseudid *Longiflagrum nasutus* is known only from the Manko mangrove wetland on Okinawa Island. It is presently unknown whether these species simply inhabit tropical/subtropical brackish waters or are specifically associated with mangrove environments. Interestingly, both species appear to be distributional outliers, with the nearest neighboring congener thousands of kilometers away: for *Nesotanais*, *N. maclaughlinae* from Palau; for *Longiflagrum*, *L. koyonense* from Thailand (Guţu and Iliffe 1989; Angsupanich 2004).

Tanaididae is one of two families commonly occurring in nearshore and brackish environments in Japan. *Zeuxo*, the most species-rich genus in this family, is distributed from Hokkaido to the Ryukyu Islands, with high population abundances from Hokkaido to Kyushu, and can be collected from many microhabitats such as laminarian holdfasts, as epibionts on seagrasses or algae (Fig. 23.1c), or sandy bottoms. Pairs of sympatric species are known, from several areas (e.g., around the Misaki Marine Biological Station), that show different pigmentation patterns (Fig. 23.3) and different frequencies of occurrence among various microhabitats, which implies habitat segregation. Many different pigmentation patterns are

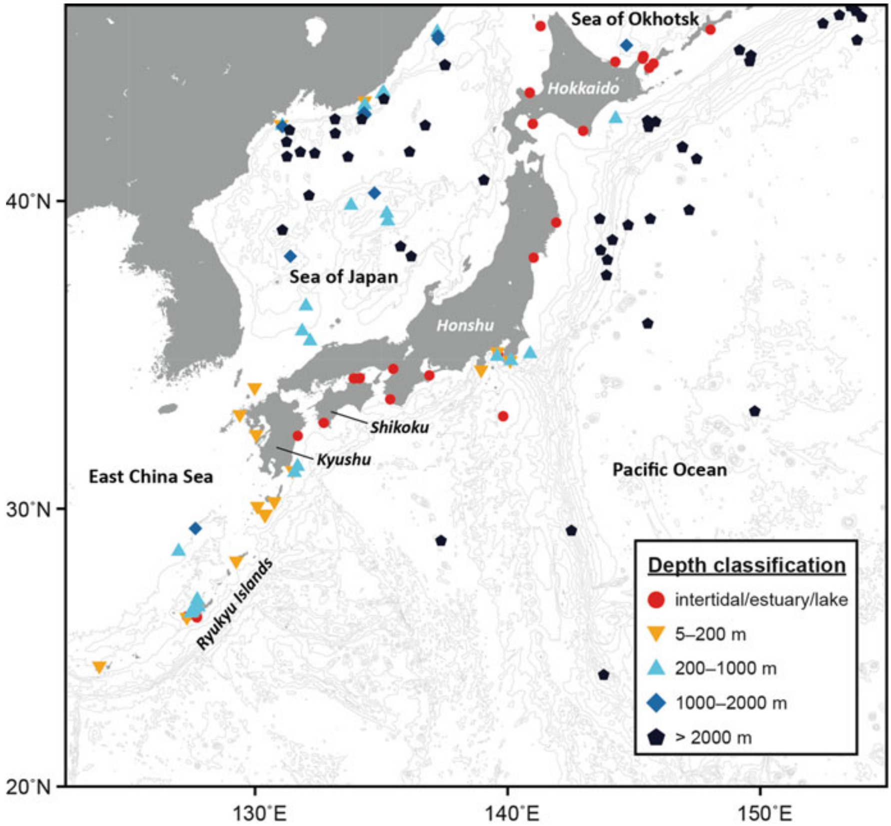

Fig. 23.2 Map showing records of tanaidaceans from around Japan (only those identified to the species level). The bathymetric contour interval is 1000 m. The map, plots, and bathymetric contour lines were generated with GMT5 software (Wessel et al. 2013) using the ETOPO1 dataset (Amante and Eakins 2009). The source of all records is given in the Appendix

evident in *Zeuxo* specimens collected in Japan, each likely corresponding to an independent species (Kakui, unpublished data). To date, three species have been reported in Japan (Table 23.1), although their type localities are far away: Addu Atoll (Maldives) for *Z. coralensis*; Fadiffolu Atoll (Maldives) for *Z. maledivensis*; Monterey Bay (USA) for *Z. normani* (Sieg 1980). The validity of the previous identifications of *Zeuxo* species in Japan are thus suspect and need to be checked.

The confamilial genus *Tanais* is also distributed throughout Japan, with high population abundances in southern Japan (in contrast to *Zeuxo*). Species in *Tanais* are positively phototactic and can be collected at night with a light trap (Naoto Jimi, personal communication). *Sinelobus* is distributed in brackish lower river regions and estuaries from northern to southern Japan. Japanese material currently treated

Fig. 23.3 Two sympatric species in *Zeuxo* found around the Misaki Marine Biological Station: ethanol-fixed specimens. (**a**) *Zeuxo* sp. 1, with the carapace having *small white marks* on a *dark background*, and a *dark* antennular article 3; this species is abundant on seagrass leaves and sandy bottoms, but rare in holdfasts. (**b**) *Zeuxo* sp. 2, with the carapace having *large white marks* and a *thick white transverse line* on a *dark background*, and a *white* antennular article 3; this species is common in holdfasts but rare on seagrass and sandy bottoms

as *Sinelobus stanfordi* actually contains at least two species, one in northern and the other in southern Japan, but they are sympatric at least in Kochi Bay, Shikoku (Kakui, unpublished data).

The other common family in coastal regions is Leptocheliidae, species of which occur abundantly intertidally in coral-rubble beds, and throughout Japan on sandy or muddy bottoms, and are also common subtidally in the shelf zone. Despite their abundance, leptocheliids have been poorly studied in Japan (Kussakin and Tzareva 1972; Ishimaru 1985; Larsen and Shimomura 2007a), with only one subtidal record (Larsen and Shimomura 2007a), and many species likely remain to be discovered.

Tanaidacean samples from the deep sea around Japan contain numerous paratanaoid species; among 15 paratanaoid families with deep-sea records (cf. Suárez-Morales et al. 2011; Bird 2012; Blazewicz-Paszkowycz et al. 2012), only Mirandotanaidae has not been reported. One neotanaoid and three apseudoid families (Neotanaidae; Apseudidae, Parapseudidae, and Sphyrapodidae) are also represented. In addition, the tanaidoid *Protanais birsteini* has been reported from hadal depths along the Kurile–Kamchatka Trench (Kudinova-Pasternak 1970; Błażewicz-Paszkowycz et al. 2015b). Sphyrapodidae is especially well represented; to date, two genera and four species have been reported from the deep sea around Japan (excluding doubtful records of *Pseudosphyrapus serratus*) (Table 23.1). Sphyrapodids have been detected all around Japan, except off the Pacific coast from eastern Hokkaido to central Honshu (Fig. 23.4) (Kakui, unpublished data). However, the distributions of the four species are more limited, as indicated in

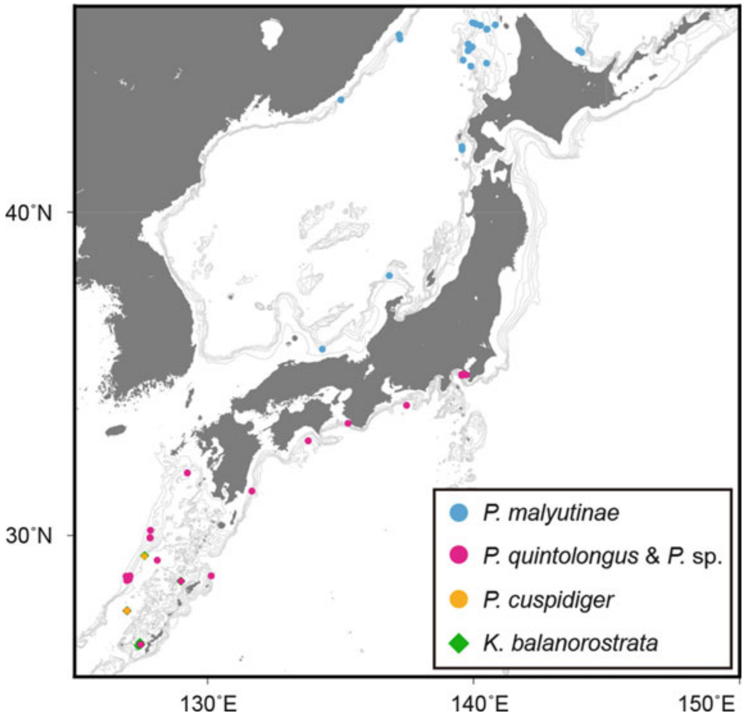

Fig. 23.4 Map showing records of sphyrapodids from around Japan. The five bathymetric contour lines indicate 200, 400, 600, 800, and 1000 m. The map, plots, and bathymetric contour lines were generated with GMT5 software (Wessel et al. 2013) using the ETOPO1 dataset (Amante and Eakins 2009). Based on data from Kakui et al. (2007); Kakui and Kajihara (2011); Błażewicz-Paszkowycz et al. (2013); and Kakui (unpublished data)

Fig. 23.4. Unidentified specimens in *Pseudosphyrapus* (*Pseudosphyrapus* sp. in Fig. 23.4) that are closely related to or possibly conspecific with *P. quintolongus* occur off the coasts of Shikoku and Honshu. The congener *P. anomalus*, with a circumpolar Arctic distribution, occurs to the north of Japan, but no other congeners have been reported from Pacific except for those around Japan. A phylogeographic study would shed light on this interesting distributional pattern.

23.3 Biology and Ecology

The biology of tanaidaceans has long interested biologists; Darwin (1872), for example, referred to their male dimorphism in *The Origin of Species*. In addition, their high abundance in bottom habitats suggests tanaidaceans might have an important role in ecosystems (Larsen et al. 2015). However, there have been relatively few studies in tanaidacean biology and ecology, perhaps because of the small size of individuals and the difficulty of identification, which relies on microscopic characters. In this section, I review knowledge on several aspects of tanaidacean biology and ecology derived from studies in Japan.

23.3.1 Morphology

Tanaidacean morphology has been studied for well over a century, as the following examples illustrate. Blanc (1884) made detailed observations on the thoracic glands associated with thread production in a tube dweller, *Heterotanais oerstedii*. Dennell (1937) illustrated feeding and respiratory structures in *Apseudes talpa*. Johnson and Attramadal (1982a) studied morphological structures and behavior related to tube dwelling in *Tanais dulongii*. Drumm (2005) examined feeding, respiratory, and cleaning behaviors and their related morphology in two kalliapseudid species, and Wirkner and Richter (2008) studied the morphology of the hemolymph vascular system among three superfamilies (*T. dulongii*, *Paradoxapseudes bermudeus*, and *Neotanais* sp.).

Several studies in Japan have also concerned morphology. In a study of the ultrastructure of the branchial chamber and epignath in *Sinelobus stanfordi*, Kikuchi and Matsumasa (1993) showed that the epithelia of both the epignath and the inner wall of the carapace (branchiostegite) are the ion-transporting type but differ in structure; the authors suggested that the latter epithelium plays a major role in osmoregulation and respiratory gas exchange. Kakui et al. (2010) observed opposing serial ridges on the inner surface of the left and right chelipeds in two *Nesotanais* species. Through behavioral observations and a comparison with similar structures in sesarmid crabs used to produce sound, that study suggested that the paired ridges in *Nesotanais* might likewise function to produce sound. In the tanaidid *Arctotanais alascensis*, Kakui et al. (2012) discovered a unique semicircular ischium on all pereopods and speculated that this character might represent a transitional stage between the circular-shaped ischium present in most tanaidaceans and complete loss of that article in tanaidids other than *A. alascensis*. Finally, in a study of the thread-producing system in the kalliapseudid apseudomorph *Phoxokalliapseudes tomiokaensis*, Kakui and Hiruta (2014) reported four distinct types of secretory system in the pereopods, with the type in pereopod 1 possibly involving secretory setae.

23.3.2 Reproductive Modes

Tanaidaceans are highly diverse in reproductive mode. Most species are gonochoristic, as are humans, with males and females engaging in sexual reproduction. However, simultaneous hermaphroditism also occurs, first reported in a species in *Apseudes* (Lang 1953). Only recently, Kakui and Hiruta (2013) showed that the simultaneously hermaphroditic *Apseudes* sp., collected from a public aquarium in Japan, can self-fertilize, the first example of self-fertilization in the crustacean class Malacostraca. The same study showed that *Apseudes* sp. becomes simultaneously hermaphroditic via a male-like phase in which only the testes are mature, which means that this species is a protandric simultaneous hermaphrodite. Specimens bearing both male and female external reproductive features have been reported in several species in genera other than *Apseudes* (cf. Rumbold et al. 2015), and some of these may similarly be functional simultaneous hermaphrodites.

Some tanaidaceans are sequential hermaphrodites. Bückle Ramírez (1965) demonstrated that *Heterotanais oerstedii* is diandrous, producing both primary males (developing directly from juveniles) and secondary males (developing by sex change from females). *Nototanais* and subsequently several other tanaidomorphs have proven similarly to be protogynous sequential hermaphrodites, changing in sex from female to male during the life cycle (cf. Rumbold et al. 2015). Although protandric sequential hermaphrodites (changing sex from male to female) have also been suspected among tanaidaceans (Wolff 1956), no case has been confirmed. Błażewicz-Paszkowycz et al. (2014) demonstrated that a single species (*Agathotanais ingolfi*) can produce two different male morphs (a sedentary form and a swimming form) (see also Bird and Holdich 1988), indicating there is much left to learn about tanaidacean life cycles. Future studies of their reproductive systems will help elucidate the evolution of reproduction in Tanaidacea, and even in Malacostraca.

23.3.3 Phenology

Tanaidacean phenology has not been well studied, though there are a few reports about several families (e.g., Aboul-Dahab et al. 2001; Fonseca and D'Incao 2003; Pennafirme and Soares-Gomes 2009). Several species appear to have an annual breeding period (Johnson and Attramadal 1982b; Fonseca and D'Incao 2003), whereas others reproduce year around (Aboul-Dahab et al. 2001). Pennafirme and Soares-Gomes (2009) showed that the life cycle can vary (e.g., presence or absence of a distinct breeding period) between tropical and subtropical populations of a single species.

Several papers have described seasonal changes in tanaidacean density in Japan. Mukai (1971) and Kito (1975) documented seasonal fluctuations associated with brown macroalgae in the genus *Sargassum*. The former study only identified tanaidaceans to the ordinal level (Tanaidacea), but the population involved probably belonged to Tanaididae; the latter study identified the populations studied as "*Anatanais normani* (Richardson)." Both studies detected an acute annual density peak of tanaidaceans during the withering season for *Sargassum* seaweeds, that is, about 2 to 4 months after the peak of the mean wet weight of the seaweeds. These results suggest that the tanaidaceans studied have a breeding period, and that this period partly overlaps the season of maximum growth and biomass accumulation of the seaweed. In a study on the distribution patterns of five peracaridans in relationship to environmental factors in a shallow, brackish lagoon, Matsumasa and Kurihara (1988) included phenological data from April 1984 to May 1985 for the tanaidid *Sinelobus stanfordi*, which inhabited the concrete wall of the lagoon embankment. The tanaidid density was quite low from April to June, increased in July, remained relatively constant until January, and then gradually decreased from February to May. As already noted here, these data may indicate a breeding period for the *Sinelobus* population in the study area, possibly from June to November or December. Nakaoka et al. (2001) studied seasonal and between-substrate variation in the mobile epibiont community (including *Zeuxo* sp., discussed under 'Feeding Habits,' following) in a multispecies seagrass bed. Although the density of *Zeuxo* sp. was close to zero most months, an acute peak occurred in July (on *Zostera marina*) or August (on *Zostera caulescens*), presumably associated with spathe use by the tanaidid. That study also found that *Zeuxo* sp. utilizes the spathes of both *Zostera* seagrass species from June to August but detected juveniles only in August. These data indicate seasonal breeding, but the duration remains unknown.

23.3.4 Feeding Habits

Tanaidaceans show diverse feeding modes and include detritivores, scavengers, browsers, raptorial carnivores, opportunists, and filter-feeders (see Larsen et al. 2015). Nakaoka (2002) discovered an interesting mode in a *Zeuxo* species in Japan. Nakaoka (2002) first found *Zeuxo* sp. inside spathes of the seagrasses *Zostera marina* and *Z. caulescens* and observed bored seeds. Through laboratory experiments and a monthly field survey, he showed that *Zeuxo* sp. consumes seagrass seeds by boring, constructs dwelling tubes in the spathes, and utilizes the spathes as the site of reproduction and as a nursery. However, *Zeuxo* sp. only seasonally utilizes the spathes, because flowering and fruiting by the seagrasses are restricted to a few summer months; during the remainder of the year, this tanaidid is nearly absent from the plants (Nakaoka et al. 2001).

Species in *Protanais* are one of the main indicators of successional stages in deep-sea wood-fall communities (McClain and Barry 2014), and are suspected of preying on *Xylophaga* wood-boring bivalves (another of the main indicators), their fecal pellets, or associated fecal bacteria (Larsen 2006; McClain and Barry 2014). Błażewicz-Paszkowycz et al. (2015b), however, found wood tissue and bacterial cells in the tanaidacean digestive tract, and nematodes and protists on the mouthparts, but no residues from bivalves. This suggests that, as with the hadal amphipod *Hirondellea gigas* (Kobayashi et al. 2012), *Protanais birsteini* may be xylophagous and contain wood-digesting enzymes.

23.3.5 Parasites

Despite high local abundances of tanaidaceans, there are only a few reports of associated parasites or commensal animals. Peritrich ciliates, foraminiferans, lasaeid bivalves, tantulocarideans, and nicothoid copepods have been reported as ecto- or mesoparasites on tanaidaceans (Warén and Carrozza 1994; Fernandez-Leborans and Sorbe 2003; Larsen 2005; Oliver et al. 2010; Błażewicz-Paszkowycz 2014), and mites, harpacticoid copepods, and ostracods have been reported as commensals in their burrows or tubes (Johnson and Attramadal 1982b; Drumm 2005). A few ecto- and mesoparasites are known from Japanese waters. Kakui and Kohtsuka (2015: Fig. 8) presented an image of unidentified peritrich ciliates parasitic on *Agathotanais misakiensis* and Błażewicz-Paszkowycz et al. (2015b) reported fibrous filamentous bacteria attached to appendages of *Protanais birsteini*. In addition, Kakui (2015b) reported copepods parasitic on the tanaidaceans *Fageapseudes* sp. and *Leptochelia* sp. collected from the East China Sea and Pacific Ocean. The copepods proved to represent two undescribed species in the nicothoid genus *Rhizorhina*, the first report of copepods parasitic on tanaidaceans from the North Pacific, and only the third worldwide.

Until recently, only nematodes and acanthocephalan larvae had been reported as endoparasites of tanaidaceans (cf. Larsen 2005). Kakui (2014) added trematodes to this list, after discovering the encysted metacercariae of a trematode inside the body cavity of the parapseudid *Longiflagrum nasutus*. Morphology and DNA sequence data placed the trematode in the family Microphallidae, species of which chiefly utilize birds as the definitive host. The true diversity of animals parasitic on tanaidaceans may be greatly underestimated.

23.3.6 Predators

Tanaidaceans have been reported in stomach contents from diverse animal groups, including crustaceans, polychaetes, sea anemones, wading birds, and fishes (Shaffer 1979; Oliver et al. 1982; Larsen 2005). In Japan, Sano et al. (1984) found that 14 species of coral reef fishes in 10 families consume tanaidaceans. Other studies (Nakagami et al. 2000; Nakamura et al. 2003; Inoue et al. 2005; Abe 2007) have found tanaidacean prey in shallow-water fishes. Tsubaki et al. (2012) reported tanaidacean as a rare prey component in stomach contents of the deep-sea fish *Caelorinchus anatirostris* (Macrouridae). Kakui (2015a) reported *Zeuxo* sp. from the stomach of an intertidal goby (*Chaenogobius annularis*) and compared the sex ratio and size distribution of this tanaidacean in the stomach with those in an environmental substratum sample. The sex ratio in the tanaidacean prey was significantly male biased, and males in the stomach were significantly larger than those in the environmental sample. Kakui (2015a) concluded that the observed sex and size bias of the prey was likely related to a prey-size preference by the fish, and perhaps to behavioral differences between male and female *Zeuxo* sp., as Johnson and Attramadal (1982b) had previously suggested for a confamilial species.

23.3.7 Ecological Surveys

Tanaidaceans are sometimes reported in ecological surveys documenting faunal assemblages. In Japan, a few such surveys have included this crustacean, including the four studies (Mukai 1971; Kito 1975; Matsumasa and Kurihara 1988; Nakaoka et al. 2001) mentioned earlier under 'Phenology'; studies on temporal and spatial variation in community structure and the effects of environmental factors in a seagrass ecosystem (Yamada et al. 2007, 2014); studies of differences in the faunal assemblage among habitats (seagrass bed–coral surface–sandy bottom) or along a depth gradient (Nakamura and Sano 2005; Nakamura et al. 2012; Takada et al. 2012); and a study comparing tanaidacean diversity and abundance among deep-sea sampling sites (Błażewicz-Paszkowycz et al. 2015a). By using experimental substrata in a brackish lagoon, Matsumasa (1994) examined the effects of secondary substratum type on small crustacean assemblages, focusing on three amphipods and a tanaidid, *Sinelobus stanfordi*, and found that the type of secondary substratum directly determined the dominant species. Larsen and Shimomura (2008) investigated the recolonization ability of tanaidaceans on a shallow sandy bottom, and found that a burrower (*Parapseudes arenamans*) had greater recolonizing ability than a tube dweller (*Paranesotanais longicephala*).

23.4 Summary and Future Perspectives

As mentioned, the numbers of tanaidacean species hitherto reported both globally and from around Japan are likely a small fraction of the actual diversities. This situation is true even among putatively common shallow-water species; for example, even well-surveyed faunas in the vicinity of marine biological stations harbor many species new to Japan or previously undetected (Fig. 23.5) (Kakui and Kohtsuka 2015; Kakui and Naruse 2015; Nakano et al. 2015). Deep-sea tanaidaceans are even more poorly known. Błażewicz-Paszkowycz et al. (2015a) detected at least 48 species in the KuramBio collection, none of which has yet been identified to the species level, and which likely include many undescribed species. Similarly, collections made during recent cruises by research/training vessels (e.g., *Nagasaki-maru*, *Seisui-maru*, *Soyo-maru*, *Tansei-maru*, *Toyoshio-maru*) around Japan include many deep-sea and some shallow-water tanaidaceans (Fig. 23.5), with a high proportion of species new to Japan or undescribed (Kakui, unpublished data). Tanaidacean systematics is also in its infancy. Further molecular studies are

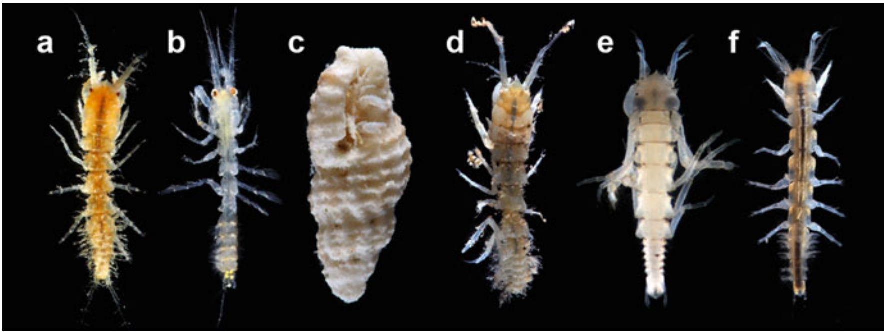

Fig. 23.5 Apseudomorphs new to Japan and/or undescribed, collected from waters in the vicinity of marine biological stations (**a**–**c**) or during research cruises (**d**–**f**); fresh specimens. (**a, d, e**) Apseudids; (**b, f**) parapseudids; (**c**) a pagurapseudid in a gastropod shell

badly needed at all taxonomic levels; even the monophyly of and relationships among the four “superfamilies” sensu Kakui et al. (2011) remain open to question.

Observations of living animals have recently elucidated various new aspects of tanaidacean biology, including a novel feeding mode (seed consumption; Nakaoka 2002), selfing (Kakui and Hiruta 2013), “skin-digging” activity in the holothuroid host by *Exspina typica* (Alvaro et al. 2011), the possibility of producing sound (Kakui et al. 2010), and thread production in apseudomorphs (Drumm 2005; Kakui and Hiruta 2014). This high rate of recent discoveries suggests that many other important discoveries remain to be made, especially with the application of approaches (e.g., breeding experiments) or techniques (e.g., bioimaging, microCT, volume electron microscopy, next-generation sequencing, micromanipulation, genome editing) not previously applied to tanaidaceans. New discoveries will not only broaden our knowledge of tanaidaceans but will also better place this minor but attractive group in the broader contexts of crustacean biology and general biology.

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Appendix: List of Literature for Fig. 23.2

Ariyama H, Ohtani M (1990) Record of tanaidacean Crustacea *Sinelobus stanfordi* (Richardson) from the Yodo River in Osaka. Nanki Seibutsu 32:23–26 (in Japanese and English abstract and captions)

Błażewicz-Paszkowycz M, Bamber RN, Jóźwiak P (2013) Tanaidaceans (Crustacea: Peracarida) from the SoJaBio joint expedition in slope and deeper waters in the Sea of Japan. Deep-Sea Res II 86–87:181–213

Błażewicz-Paszkowycz M, Kobyłecka E, Jennings RN (2015) Redescription of wood-associated tanaidacean *Protanais birsteini* (Kudinova-Pasternak, 1970) and its relationship within the Tanaididae. Deep-Sea Res II 111:333–342

Edger GJ (2008) Shallow water Tanaidae (Crustacea: Tanaidacea) of Australia. Zootaxa 1836:1–92

Ishimaru S (1985) A new species of *Leptochelia* (Crustacea, Tanaidacea) from Japan, with a redescription of *L. savignyi* (Krøyer, 1842). Publ Seto Mar Biol Lab 30:241–267

Kakui K, Hiruta C (2014) Diverse pereopodal secretory systems implicated in thread production in an apseudomorph tanaidacean crustacean. J Morphol 275:1041–1052

Kakui K, Kajihara H (2011) *Pseudosphyrapus cuspidiger* sp. nov. from the Nansei Islands, Japan, with a supplementary description of *Kudinopasternakia balanorostrata* Kakui, Kajihara and Mawatari, 2007 (Crustacea: Tanaidacea: Apseudomorpha: Sphyrapodidae). Bull Natl Nat Sci Ser A Suppl 5:53–70

Kakui K, Kohtsuka H (2015) Two new shallow-water species of *Agathotanais* (Crustacea: Tanaidacea) from Japan. Species Divers 20:45–58

Kakui K, Naruse T (2015) *Indoapseudes bamberi* sp. nov. (Crustacea: Tanaidacea: Pagurapseudidae: Hodometricinae) from Iriomote Island, Ryukyu Islands, southwestern Japan. Zootaxa 3995:138–148

Kakui K, Yamasaki H (2013) Nototanaids (Crustacea: Tanaidacea) from Japan, with the description of a new species of *Nototanoides*. Species Divers 18:245–254

Kakui K, Kajihara H, Mawatari SF (2007) Two new sphyrapodid species (Crustacea: Tanaidacea: Apseudomorpha) from southwestern Japan. Zootaxa 1563:37–54

Kakui K, Kajihara H, Mawatari SF (2010) A new species of *Nesotanais* Shiino, 1968 (Crustacea, Tanaidacea) from Japan, with a key to species and a note on male chelipeds. ZooKeys 33:1–17

Kakui K, Katoh T, Hiruta SF, Kobayashi N, Kajihara H (2011) Molecular systematics of Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of suborder/superfamily-level classification. Zool Sci 28:749–757

Kakui K, Kobayashi N, Mawatari SF (2012) Phylogenetic position of *Arctotanais* in the suborder Tanaidomorpha (Peracarida: Tanaidacea). J Crustacean Biol 32:127–139

Kakui K, Tomioka S, Yamasaki H (2014) Tanaidaceans from Rishiri Island (Crustacea: Peracarida). Rishiri Stud 33:7–12 (in Japanese with English abstract)

Kudinova-Pasternak RK (1966a) On a new abyssal tanaidacean from the Pacific ultra-abyssals. Crustaceana 12:257–260

Kudinova-Pasternak RK (1966b) Tanaidacea (Crustacea) of the Pacific ultra-abyssals. Zool Zh 45:518–535 (in Russian with English abstract)

Kudinova-Pasternak RK (1970) [Tanaidacea of the Kurile-Kamchatka Trench]. Tr Inst Okeanol 86:341–381 (in Russian)

Kudinova-Pasternak RK (1976) Additional notes of the fauna of Tanaidacea (Crustacea, Malacostraca) of the deep water trenches. Tr Inst Okeanol 99:115–125 (in Russian with English abstract)

Kudinova-Pasternak RK (1978) Tanaidacea (Crustacea, Malacostraca) from the deep-sea trenches of the western part of the Pacific. Tr Inst Okeanol 108:115–135 (in Russian with English abstract)

Kudinova-Pasternak RK (1984) The Tanaidacea (Crustacea, Malacostraca) of the Sea of Japan. Zool Zh 63:828–838 (in Russian with English abstract)

Kussakin OG, Tzareva LA (1972) Tanaidacea from the coastal zones of the Middle Kurile Islands. Crustaceana Suppl 3:237–245

Lang K (1966) Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen 2. Die Gattung *Parapseudes* G. O. Sars. Ark Zool Ser 2 18:549–566 + 1 pl

Larsen K, Shimomura M (2006) Tanaidacea (Crustacea: Peracarida) from Japan. I. Apseudomorpha from the East China Sea, Seto Inland Sea, and Nansei Islands. Zootaxa 1341:29–48

Larsen K, Shimomura M (2007a) Tanaidacea (Crustacea: Peracarida) from Japan. II. Tanaidomorpha from the East China Sea, the West Pacific Ocean and the Nansei Islands. Zootaxa 1464:1–43

Larsen K, Shimomura M (eds) (2007b) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile-Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland

Larsen K, Shimomura M (2008) Tanaidacea (Crustacea: Peracarida) from Japan. IV. Shallow-water species from Akajima with notes on the recolonization potential of tanaids. Zootaxa 1678:1–24

Larsen K, Shimomura M (2009) Tanaidacea (Crustacea: Peracarida) from Japan. V. A new species of *Chauliopleona* from Nagasaki, Kyushu. Species Divers 14:49–59

Matsumasa M (1994) Effect of secondary substrate on associated small crustaceans in a brackish lagoon. J Exp Mar Biol Ecol 176:245–256

Nunomura N (1985) Marine tanaid and isopod crustaceans off Kagawa Prefecture, Seto Inland Sea, Japan. Spec Publ Mukaishima Mar Biol Stn 1985:101–112

Nunomura N (2005) A new species of genus *Apseudes* (Tanaidacea: Apseudidae) Okinawa, southern Japan. Bull Toyama Sci Mus 28:25–31

Saito N (1996) Notes on poorly known species of the crustaceans recorded from Kaminato Harbor, Hachijo Island, the Izu Islands. I.O.P. Diving News 7:2–5 (in Japanese with English abstract and captions)

Shiino SM (1937) On *Apseudes nipponicus* n. sp. (Crustacea, Tanaidacea). Annot Zool Jpn 16:53–62

Shiino SM (1951a) Note on three species of Tanaidae from Japanese Coast. Misc Rep Res Inst Nat Resour 19–21:32–38 (in Japanese)

Shiino SM (1951b) On two new species of the family Apseudidae found at Seto. Rep Fac Fish Prefect Univ Mie 1:12–25

Shiino SM (1952) A new genus and two new species of the order Tanaidacea found at Seto. Publ Seto Mar Biol Lab 2:53–68

Shiino SM (1966) On *Kalliapseudes* (*Kalliapseudes*) *tomiokaensis* sp. nov. (Crustacea: Tanaidacea) from Japanese waters. Rep Fac Fish Prefect Univ Mie 5:473–488

Sieg J (1980) Taxonomische Monographie der Tanaidae Dana 1849 (Crustacea: Tanaidacea). Abh Senckenb Naturforsch Ges 537:1–267

Stephensen K (1936) A tanaid (*Tanais stanfordi* Richardson) found in fresh water in the Kurile Islands, with taxonomic remarks on the genus *Tanais* sunsu lat. (*Tanais* Audouin et Milne-Edward 1829, and *Anatanais* Nordenstam 1930). Annot Zool Jpn 15:361–373

Uéno M (1936) Crustacea Malacostra collected in the lakes of the Island of Kunasiri. Bull Biogeogr Soc Jpn 6:247–252

References

Abe F (2007) Studies on the use of eelgrass-shaped substrate reef by the juvenile red sea bream, *Pagrus major*, and other organisms. Bull Mar Sci Fish Kochi Univ 25:5–57 [in Japanese with English abstract]

Aboul-Dahab HM, Hussein MA, Soliman FE, Ismail TG (2001) Reproductive aspects on the peracarid crustaceans *Leptochelia erythraea* and *Cyproidea ornata*, from the Red Sea, Egypt. Bull Fac Sci Assiut Univ 30(1-E):23–36

Alvaro MC, Błażewicz-Paszkowycz M, Davey M, Schiaparelli S (2011) Skin-digging tanaids: the unusual parasitic bahaviour of *Exspina typica* in Antarctic waters and worldwide deep basins. Antarct Sci 23:343–348

Amante C, Eakins BW (2009) ETOPO1 1 arc-minute global relief model: procedures, data sources and analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA. doi:10.7289/V5C8276M. Accessed 15 Jul 2015

Anderson G (2013) Tanaidacea—thirty years of scholarship (vers. 1.1, May 2013). http://peracarida.usm.edu/TanaidaceaText.pdf. Accessed 1 Dec 2014

Angsupanich S (2004) A new species of *Longiflagrum* (Tanaidacea, Parapseudidae), from Songkhla Lagoon, Thailand. Crustaceana 77:849–860

Ariyama H, Ohtani M (1990) Record of tanaidacean Crustacea *Sinelobus stanfordi* (Richardson) from the Yodo River in Osaka. Nanki Seibutsu 32:23–26 [in Japanese with English abstract]

Bamber RN (2007) Suborder Apseudomorpha Sieg, 1980 and Neotanaidomorpha Sieg, 1980. In: Larsen K, Shimomura M (eds) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile–Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland, pp 13–40

Barnard JL (1970) Benthic ecology of Bahia de San Quintin Baja California. Smithson Contrib Zool 44:1–60

Bird GJ (2007a) Families Anarthruridae Lang, 1971, Colletteidae Larsen & Wilson, 2002, and Leptognathiidae Sieg, 1976. In: Larsen K, Shimomura M (eds) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile–Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland, pp 61–85

Bird GJ (2007b) Family *incertae sedis*. In: Larsen K, Shimomura M (eds) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile–Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland, pp 121–149

Bird GJ (2012) A new leptochelioid family, Heterotanoididae (Crustacea: Peracarida: Tanaidacea), and a new species of *Heterotanoides* from New Zealand. Zootaxa 3481:1–26

Bird GJ, Holdich DM (1988) Deep-sea Tanaidacea (Crustacea) of the North-east Atlantic: the tribe Agathotanaini. J Nat Hist 22:1591–1621

Blanc H (1884) Contribution a l'histoire naturelle des asellotes hétéropodes observations faites sur la *Tanais œrstedii*. Krœyer Reclam Zool Suisse Sér I 1:189–258 + pls. X–XII

Błażewicz-Paszkowycz M (2007) Family Nototanaidae Sieg, 1976 and Typhlotanaidae Sieg, 1984. In: Larsen K, Shimomura M (eds) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile–Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland, pp 101–120

Błażewicz-Paszkowycz M (2014) 5.19. Tanaidacea. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz CD, Van de Putte AP, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Huettmann F, Post A, Ropert-Coudert Y (eds) Biogeographic atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 173–180

Blazewicz-Paszkowycz M, Bamber R, Anderson G (2012) Diversity of Tanaidacea (Crustacea: Peracarida) in the world's oceans—how far have we come? PLoS ONE 7. doi: 10.1371/journal.pone.0033068

Błażewicz-Paszkowycz M, Bamber RN, Jóźwiak P (2013) Tanaidaceans (Crustacea: Peracarida) from the SoJaBio joint expedition in slope and deeper waters in the Sea of Japan. Deep-Sea Res II 86–87:181–213

Błażewicz-Paszkowycz M, Jenning RM, Jeskulke K, Brix S (2014) Discovery of swimming males of Paratanaoidea (Tanaidacea). Pol Polar Res 35:415–453

Błażewicz-Paszkowycz M, Pabis K, Jóźwiak P (2015a) Tanaidacean fauna of the Kuril–Kamchatka Trench and adjacent abyssal plain—abundance, diversity and rare species. Deep-Sea Res II 111:325–332

Błażewicz-Paszkowycz M, Kobyłecka E, Jennings RN (2015b) Redescription of wood-associated tanaidacean *Protanais birsteini* (Kudinova-Pasternak, 1970) and its relationship within the Tanaididae. Deep-Sea Res II 111:333–342

Bückle Ramírez LF (1965) Untersuchungen über die Biologie von *Heterotanais oerstedi* Kröyer (Crustacea, Tanaidacea). Z Morph Ökol Tiere 55:714–782

Chapman MA, Lewis MH, Winterbourn MJ (2011) Guide to the freshwater Crustacea of New Zealand. New Zealand Freshwater Sciences Society, Christchurch

Darwin CR (1872) The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life, 6th edn. John Murray, London

Delille D, Guidi LD, Soyer J (1985) Nutrition of *Allotanais hirsutus* (Crustacea: Tanaidacea) at Kerguelen Island. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 378–380

Dennell R (1937) On the feeding mechanism of *Apseudes talpa*, and evolution of the peracaridan feeding mechanisms. Trans R Soc Edinb 59:57–78

Drumm DT (2005) Comparison of feeding mechanisms, respiration, and cleaning behavior in two kalliapseudids, *Kalliapseudes macsweenyi* and *Psammokalliapseudes granulosus* (Peracarida: Tanaidacea). J Crustacean Biol 25:203–211

Drumm DT (2010) Phylogenetic relationships of Tanaidacea (Eumalacostraca: Peracarida) inferred from three molecular loci. J Crustacean Biol 30:692–698

Fernandez-Leborans G, Sorbe J-C (2003) A new protozoan of the genus *Cothurnia* (Ciliophora, Peritrichia), epibiont on the marine tanaid *Halmyrapseudes spaansi* (Crustacea Peracarida) from the French Guiana (SE America). Zool Anz 242:267–275

Fonseca DB, D'Incao F (2003) Growth and reproductive parameters of *Kalliapseudes schubartii* in the estuarine region of the Lagoa dos Patos (southern Brazil). J Mar Biol Assoc UK 83:931–935

Gamo S (1984) A new remarkably giant tanaid, *Gigantapseudes maximus* sp. nov. (Crustacea) from the abyssal depths far off southeast of Mindanao, the Philippines. Sci Rep Yokohama Natl Univ Sect II 31:1–12

Giri C, Ochieng E, Tieszen LL, Zhu Z, Singh A, Loveland T, Masek J, Duke N (2011) Status and distribution of mangrove forests of the world using earth observation satellite data. Global Ecol Biogeogr 20:154–159

Guţu M, Iliffe TM (1989) Description of two new species of Tanaidacea (Crustacea) from the marine water caves of the Palau Islands (Pacific Ocean). Trav Mus Hist Nat Grigore Antipa 30:169–180

Guţu M, Iliffe TM (2011) *Leptochelia vatulelensis* (Crustacea: Tanaidacea), a new species from anchialine caves of the south-western Pacific. Trav Mus Natl Hist Nat Grigore Antipa 54:351–363

Hassack E, Holdich DM (1987) The tubicolous habit amongst the Tanaidacea (Crustacea, Peracarida) with particular reference to deep-sea species. Zool Scr 16:223–233

Inoue T, Suda Y, Sano M (2005) Food habits of fishes in the surf zone of a sandy beach at Sanrimatsubara, Fukuoka Prefecture, Japan. Ichthyol Res 52:9–14

Ishimaru S (1985) A new species of *Leptochelia* (Crustacea, Tanaidacea) from Japan, with a redescription of *L. savignyi* (Krøyer, 1842). Publ Seto Mar Biol Lab 30:241–267

Johnson SB, Attramadal YG (1982a) A functional-morphological model of *Tanais cavolinii* Milne-Edwards (Crustacea, Tanaidacea) adapted to a tubicolous life-strategy. Sarsia 67:29–42

Johnson SB, Attramadal YG (1982b) Reproductive behaviour and larval development of *Tanais cavolinii* (Crustacea: Tanaidacea). Mar Biol 71:11–16

Kakui K (2014) A novel transmission pathway: first report of a larval trematode in a tanaidacean crustacean. Fauna Ryukyuana 17:13–22

Kakui K (2015a) First report of *Zeuxo* sp. (Crustacea: Tanaidacea) as prey for the forktongue goby, *Chaenogobius annularis* Gill, 1859. Rishiri Stud 34:1–6 [in Japanese with English abstract]

Kakui K (2015b) Descriptions of two new species of *Rhizorhina* Hansen, 1892 (Copepoda: Siphonostomatoida: Nicothoidae) parasitic on tanaidacean crustaceans, with a note on their phylogenetic position. Syst Parasitol (in press)

Kakui K, Angsupanich S (2012) *Birdotanais songkhlaensis*, a new genus and species of Nototanaidae (Crustacea: Tanaidacea) from Thailand. Raffles B Zool 60:421–432

Kakui K, Hiruta C (2013) Selfing in a malacostracan crustacean: why a tanaidacean but not decapods. Naturwissenschaften 100:891–894

Kakui K, Hiruta C (2014) Diverse pereopodal secretory systems implicated in thread production in an apseudomorph tanaidacean crustacean. J Morphol 275:1041–1052

Kakui K, Kajihara H (2011) *Pseudosphyrapus cuspidiger* sp. nov. from the Nansei Islands, Japan, with a supplementary description of *Kudinopasternakia balanorostrata* Kakui, Kajihara and Mawatari, 2007 (Crustacea: Tanaidacea: Apseudomorpha: Sphyrapodidae). Bull Natl Mus Nat Sci Ser A Suppl 5:53–70

Kakui K, Kohtsuka H (2015) Two new shallow-water species of *Agathotanais* (Crustacea: Tanaidacea) from Japan. Species Divers 20:45–58

Kakui K, Naruse T (2015) *Indoapseudes bamberi* sp. nov. (Crustacea: Tanaidacea: Pagurapseudidae: Hodometricinae) from Iriomote Island, Ryukyu Islands, southwestern Japan. Zootaxa 3995:138–148

Kakui K, Yamasaki H (2013) Nototanaids (Crustacea: Tanaidacea) from Japan, with the description of a new species of *Nototanoides*. Species Divers 18:245–254

Kakui K, Kajihara H, Mawatari SF (2007) Two new sphyrapodid species (Crustacea: Tanaidacea: Apseudomorpha) from southwestern Japan. Zootaxa 1563:37–54

Kakui K, Kajihara H, Mawatari SF (2010) A new species of *Nesotanais* Shiino, 1968 (Crustacea, Tanaidacea) from Japan, with a key to species and a note on male chelipeds. ZooKeys 33:1–17

Kakui K, Katoh T, Hiruta SF, Kobayashi N, Kajihara H (2011) Molecular systematics of Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of suborder/superfamily-level classification. Zool Sci 28:749–757

Kakui K, Kobayashi N, Kajihara H (2012) Phylogenetic position of *Arctotanais* in the suborder Tanaidomorpha (Peracarida: Tanaidacea). J Crustacean Biol 32:127–139

Kakui K, Tomioka S, Yamasaki H (2014) Tanaidaceans from Rishiri Island (Crustacea: Peracarida). Rishiri Stud 33:7–12 [in Japanese with English abstract]

Kikuchi S, Matsumasa M (1993) Two ultrastructurally distinct types of transporting tissues, the branchiostegal and the gill epithelia, in an estuarine tanaid, *Sinelobus stanfordi* (Crustacea, Peracarida). Zoomorphology 113:253–260

Kito K (1975) Preliminary report on the phytal animals in the *Sargassum confusum* region in Oshoro Bay, Hokkaido. J Fac Sci Hokkaido Univ Ser VI Zool 20:141–158

Kobayashi H, Hatada Y, Tsubouchi T, Nagahama T, Takami H (2012) The hadal amphipod *Hirondellea gigas* possessing a unique cellulase for digesting wooden debris buried in the deepest seafloor. PLoS ONE 7. doi: 10.1371/journal.pone.0042727

Kudinova-Pasternak RK (1966a) On a new abyssal tanaidacean from the Pacific ultra-abyssals. Crustaceana 12:257–260

Kudinova-Pasternak RK (1966b) Tanaidacea (Crustacea) of the Pacific ultra-abyssals. Zool Zh 45:518–535 [in Russian with English abstract]

Kudinova-Pasternak RK (1970) Tanaidacea of the Kurile–Kamchatka Trench. Tr Inst Okeanol 86:341–381 [in Russian]

Kudinova-Pasternak RK (1976) Additional notes of the fauna of Tanaidacea (Crustacea, Malacostraca) of the deep water trenches. Tr Inst Okeanol 99:115–125 [in Russian with English abstract]

Kudinova-Pasternak RK (1978) Tanaidacea (Crustacea, Malacostraca) from the deep-sea trenches of the western part of the Pacific. Tr Inst Okeanol 108:115–135 [in Russian with English abstract]

Kudinova-Pasternak RK (1984) The Tanaidacea (Crustacea, Malacostraca) of the Sea of Japan. Zool Zh 63:828–838 [in Russian with English abstract]

Kussakin OG, Tzareva LA (1972) Tanaidacea from the coastal zones of the Middle Kurile Islands. Crustaceana Suppl 3:237–245

Lang K (1953) *Apseudes hermaphroditicus* n. sp. A hermaphroditic tanaide from the Antarctic. Ark Zool Ser 2(4):341–350 + 4 pls

Larsen K (2005) Deep-sea Tanaidacea (Peracarida) from the Gulf of Mexico. Brill, Leiden

Larsen K (2006) Tanaidacea (Crustacea; Peracarida) from chemically reduced habitats—the hydrothermal vent system of the Juan de Fuca Ridge, Escabana Trough and Gorda Ridge, northeast Pacific. Zootaxa 1164:1–33

Larsen K (2007) Family Agathotanaidae Lang, 1971a. In: Larsen K, Shimomura M (eds) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile–Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland, pp 41–60

Larsen K (2012) A new family, genus and species of apseudomorphan Tanaidacea (Crustacea: Peracarida) from the Caribbean Sea. J Mar Biol Assoc UK 92:1089–1093

Larsen K, Shimomura M (2006) Tanaidacea (Crustacea: Peracarida) from Japan. I. Apseudomorpha from the East China Sea, Seto Inland Sea, and Nansei Islands. Zootaxa 1341:29–48

Larsen K, Shimomura M (2007a) Tanaidacea (Crustacea: Peracarida) from Japan. II. Tanaidomorpha from the East China Sea, the West Pacific Ocean and the Nansei Islands. Zootaxa 1464:1–43

Larsen K, Shimomura M (eds) (2007b) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile–Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland

Larsen K, Shimomura M (2008) Tanaidacea (Crustacea: Peracarida) from Japan. IV. Shallow-water species from Akajima with notes on the recolonization potential of tanaids. Zootaxa 1678:1–24

Larsen K, Shimomura M (2009) Tanaidacea (Crustacea: Peracarida) from Japan. V. A new species of *Chauliopleona* from Nagasaki, Kyushu. Species Divers 14:49–59

Larsen K, Guţu M, Sieg J (2015) Order Tanaidacea Dana, 1849. In: Vaupel Klein JC von, Charmantier-Daures M, Schram FR (eds) The Crustacea. Revised and updated, as well as extended from the Traité de Zoologie 5. Brill, Leiden, pp 249–329

Matsumasa M (1994) Effect of secondary substrate on associated small crustaceans in a brackish lagoon. J Exp Mar Biol Ecol 176:245–256

Matsumasa M, Kurihara Y (1988) Distribution patterns of benthic small crustaceans and the environmental factors in a brackish shallow-water lagoon, Gamō lagoon. Benthos Res 33 (34):33–41 [in Japanese with English abstract]

McClain C, Barry J (2014) Beta-diversity on deep-sea wood falls reflects gradients in energy availability. Biol Lett 10. doi: 10.1098/rsbl.2014.0129

McLelland JA (2007) Family Pseudotanaidae Sieg, 1976. In: Larsen K, Shimomura M (eds) Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile–Kamchatka Trench and Japan Trench. Zootaxa 1599. Magnolia Press, Auckland, pp 87–99

Mukai H (1971) The phytal animals on the thalli of *Sargassum serratifolium* in the *Sargassum* region, with reference to their seasonal fluctuations. Mar Biol 8:170–182

Nakagami M, Takatsu T, Matsuda T, Takahashi T (2000) Feeding on harpacticoid copepods by marbled sole *Pleuronectes yokohamae* juveniles in the coastal areas of Tsugaru Strait, Hokkaido. Nippon Suisan Gakk 66:818–824 [in Japanese with English abstract]

Nakamura Y, Sano M (2005) Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. Fish Sci 71:543–550

Nakamura Y, Horinouchi M, Nakai T, Sano M (2003) Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. Ichthyol Res 50:15–22

Nakamura Y, Hirota K, Shibuno T, Watanabe Y (2012) Variability in nursery function of tropical seagrass beds during fish ontogeny: timing of ontogenetic habitat shift. Mar Biol 159:1305–1315

Nakano H, Kakui K, Kajihara H, Shimomura M, Jimi N, Tomioka S, Tanaka H, Yamasaki H, Tanaka M, Izumi T, Okanishi M, Yamada Y, Shinagawa H, Sato T, Tsuchiya Y, Omori A, Sekifuji M, Kohtsuka H (2015) JAMBIO Coastal Organism Joint Surveys reveals undiscovered biodiversity around Sagami Bay. Reg Stud Mar Sci 2(suppl):77–81

Nakaoka M (2002) Predation on seeds of seagrasses *Zostera marina* and *Zostera caulescens* by a tanaid crustacean *Zeuxo* sp. Aquat Bot 72:99–106

Nakaoka M, Toyohara T, Matsumasa M (2001) Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan. Mar Ecol 22:379–395

Nunomura N (1985) Marine tanaid and isopod crustaceans off Kagawa Prefecture, Seto Inland Sea, Japan. Spec Publ Mukaishima Mar Biol Stn 1985:101–112

Nunomura N (2005) A new species of genus *Apseudes* (Tanaidacea: Apseudidae) Okinawa, southern Japan. Bull Toyama Sci Mus 28:25–31

Oliver JS, Oakden JM, Slattery PN (1982) Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft-bottom communities. Mar Ecol Prog Ser 7:179–184

Oliver PG, Holmes AM, Killeen IJ, Turner JA (2010) Marine bivalve shells of the British Isles (Mollusca: Bivalvia). Amgueddfa Cymru, National Museum Wales. http://naturalhistory.museumwales.ac.uk/britishbivalves/browserecord.php?-recid=276. Accessed 6 Aug 2015

Pennafirme S, Soares-Gomes A (2009) Population biology and reproduction of *Kalliapseudes schubartii* Mañé-Garzón, 1949 (Peracarida, Tanaidacea) in a tropical coastal lagoon, Itaipu, southeastern Brazil. Crustaceana 82:1509–1526

Rumbold CE, Obenat SM, Leonardi MS, Spivak ED (2015) Intersex in the gonochoristic crustacean *Tanais dulongii* (Audouin, 1826) (Peracarida: Tanaidacea: Tanaididae): a comparison of external reproductive characteristics. J Nat Hist 49:775–788

Saito N (1996) Notes on poorly known species of the crustaceans recorded from Kaminato Harbor, Hachijo Island, the Izu Islands. IOP Diving News 7:2–5 [in Japanese with English abstract]

Sánchez-García A, Penãlver E, de la Fuente RP, Delclós X (2015) A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: palaeobiological implications. J Syst Palaeontol 13:645–676

Sano M, Shimizu M, Nose Y (1984) Food habits of teleostean reef fishes in Okinawa Island, southern Japan. Univ Mus Univ Tokyo Bull 25:1–128

Shaffer PL (1979) The feeding biology of *Podarke pugettensis* (Polychaeta: Hesionidae). Biol Bull 156:343–355

Shiino SM (1937) On *Apseudes nipponicus* n. sp. (Crustacea, Tanaidacea). Annot Zool Jpn 16:53–62

Shiino SM (1951a) Note on three species of Tanaidae from Japanese Coast. Misc Rep Res Inst Nat Resour 19–21:32–38 [in Japanese]

Shiino SM (1951b) On two new species of the family Apseudidae found at Seto. Rep Fac Fish Prefect Univ Mie 1:12–25

Shiino SM (1952) A new genus and two new species of the order Tanaidacea found at Seto. Publ Seto Mar Biol Lab 2:53–68

Shiino SM (1963) Tanaidacea collected by Naga Expedition in the Bay of Nha-Trang, South Viet-Nam. Rep Fac Fish Prefect Univ Mie 4:437–507

Shiino SM (1966) On *Kalliapseudes* (*Kalliapseudes*) *tomiokaensis* sp. nov. (Crustacea: Tanaidacea) from Japanese waters. Rep Fac Fish Prefect Univ Mie 5:473–488

Sieg J (1980) Taxonomische Monographie der Tanaidae Dana 1849 (Crustacea: Tanaidacea). Abh Senckenb Naturforsch Ges 537:1–267

Stephensen K (1936) A tanaid (*Tanais stanfordi* Richardson) found in fresh water in the Kurile Islands, with taxonomic remarks on the genus *Tanais* sensu lat. (*Tanais* Audouin et Milne-Edwards 1829, and *Anatanais* Nordenstam 1930). Annot Zool Jpn 15:361–373

Suárez-Morales E, Londoño-Mesa M, Heard RW (2011) Discovery of a new genus of tanaidacean (Crustacea: Tanaidacea: Mirandotanaidae) found associated with a deep-sea terebellid polychaete. Contrib Zool 80:157–167

Takada Y, Abe O, Sibuno T (2012) Variations in cryptic assemblages in coral-rubble interstices at a reef slope in Ishigaki Island, Japan. Fish Sci 78:91–98

Tsubaki K, Takeda M, Morii Y, Hashimoto J (2012) Feeding habits of the macrourid fish, *Caelorinchus anatirostris* from the upper continental slope southwest of Nagasaki, Japan. Jpn J Benthos 67:9–14 [in Japanese with English abstract]

Warén A, Carrozza F (1994) *Arculus sykesi* (Chaster), a leptonacean bivalve living on a tanaid Crustacea in the Gulf of Genova. Boll Malacol 29:303–306

Wessel P, Smith WHF, Scharroo R, Luis J, Wobbe F (2013) Generic Mapping Tools: improved version released. EOS Trans Am Geophys Union 94:409–410

Wirkner CS, Richter S (2008) Morphology of the haemolymph vascular system in Tanaidacea and Cumacea:—implications for the relationships of "core group" Peracarida (Malacostraca; Crustacea). Arthropod Struct Dev 37:141–154

Wolff T (1956) Crustacea Tanaidacea from depths exceeding 6000 meters. Galathea Rep 2:187–241

Yamada K, Hori M, Tanaka Y, Hasegawa N, Nakaoka M (2007) Temporal and spatial macrofaunal community changes along a salinity gradient in seagrass meadows of Akkeshi-ko estuary and Akkeshi Bay, northern Japan. Hydrobiologia 592:345–358

Yamada K, Tanaka Y, Era T, Nakaoka M (2014) Environmental and spatial controls of macroinvertebrate functional assemblages in seagrass ecosystems along the Pacific coast of northern Japan. Global Ecol Conserv 2:47–61

Chapter 24
Diversity of Freshwater and Marine Bryozoans in Japan

Masato Hirose

Abstract Bryozoans comprise a phylum of clonal, modular animals that inhabit marine and freshwater environments, with more than 6000 living species described. The long latitudinal range of Japan across several climatic zones and a complex nearshore bottom topography have resulted in high bryozoan diversity, which may exceed 1000 species. Bryozoan diversity has been studied in Japan from the late nineteenth century to the present. Revisional studies of historical collections and taxonomic inventories in previously uninvestigated localities and poorly studied habitats such as the intertidal zone and deep sea will increase our knowledge of bryozoan diversity in Japanese waters. This chapter reviews the history of Japanese bryozoan research and summarizes the diversity of bryozoans in this region.

Keywords Ectoprocta • Gymnolaemata • Stenolaemata • Phylactolaemata • Marine invertebrates

24.1 Introduction to Bryozoans

Phylum Bryozoa (Ectoprocta) is a group of sessile, modular, clonal animals that inhabit marine and freshwater environments. Bryozoans form colonies of various morphologies on many kinds of substrate. The zooids (Fig. 24.1) in a colony have a feeding organ called the lophophore, with ciliated tentacles surrounding the mouth; a complete, U-shaped digestive tract with the anus outside the lophophore; and a cuticular exoskeleton that is often calcified.

Bryozoans occur in all oceans, from the intertidal zone to abyssal depths, but reach maximum species diversities in rocky nearshore shelf habitats in the 0- to 100-m depth interval (Gordon 1999). About 6,000 living species have been described from marine environments, and about 20,000 species overall, including fossil species (Gordon 1999; Bock and Gordon 2013); extant diversity probably exceeds 8,000 species (Gordon 2000; Ryland 2005). Fossil bryozoan species are

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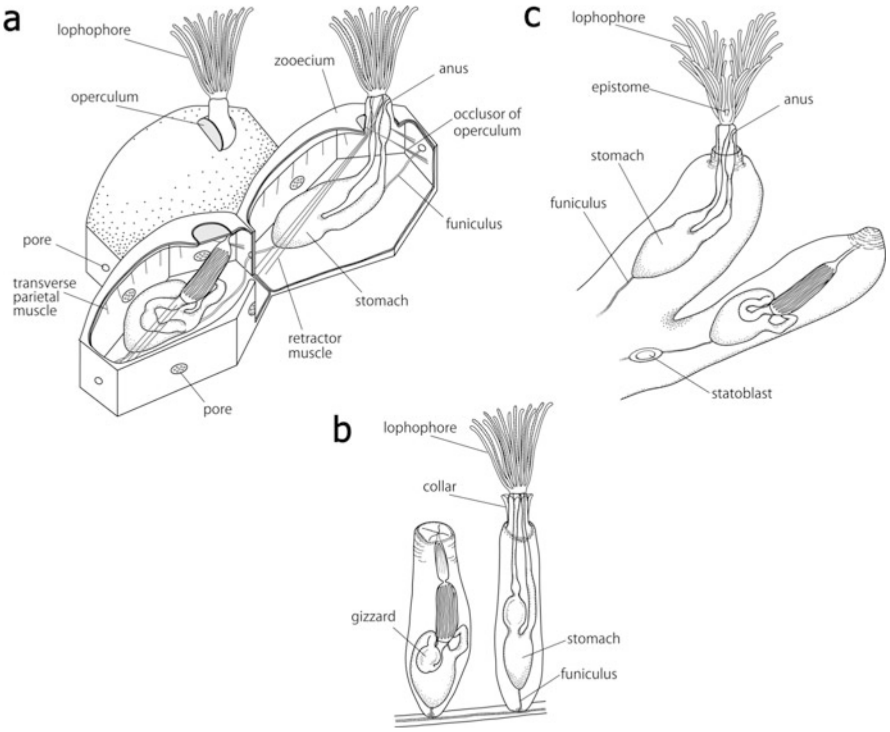

Fig. 24.1 Forms of bryozoan zooids. **a** Cheilostomata. **b** Ctenostomata. **c** Phylactolaemata

known from the early Ordovician and are abundant in the Paleozoic. Because of their long fossil record, high diversity, broad distribution, and important roles in sessile communities, marine bryozoans have attracted considerable attention from marine ecology, paleoecology, and environmental science.

Modern bryozoans are divided into three classes: Gymnolaemata (primarily marine), Stenolaemata (exclusively marine), and Phylactolaemata (exclusively in freshwater). Most orders in the class Stenolaemata are extinct; Cyclostomata is the only order found in present-day oceans, with about 540 living species. Order Cheilostomata in class Gymnolaemata is the most speciose group of bryozoans in modern marine environments, with about 4900 living species. Both Cyclostomata and Cheilostomata have zooids with calcified walls, and characters of the calcified exoskeleton are of primary importance for identification and classification. The order Ctenostomata in Gymnolaemata is less diverse, with only about 300 species, most of which are marine, although about 20 species inhabit brackish or freshwater habitats. Ctenostome colonies are not calcified, but are composed of cylindrical, elliptical, or box-like zooids having a cuticular wall; external zooid morphology and internal features such as the digestive tract are important for identification and classification.

Species in Phylactolaemata are restricted to freshwater habitats and show much lower diversity than marine bryozoans, with only about 80 species worldwide (Wood and Okamura 2005). Phylactolaemate colonies have a branched, tubular morphology or develop as compact gelatinous masses, but are not calcified. Characters such as the color and the texture of the colony surface, formed of sand grains and chitin fibers, have been used to identify phylactolaemate genera and species, but these characters vary ecophenotypically. Phylactolaemates form asexual encapsulated dormant bodies, called statoblasts, that are generally resistant to cooling and drying, and germinate under favorable conditions following an obligate period of dormancy, in response to a variety of factors such as increases in water temperature or light. There are two types of statoblasts: a free-floating buoyant statoblast (floatoblast) and a sessile statoblast (sessoblast). Statoblasts provide characters highly useful in phylactolaemate taxonomy and identification; their gross morphology and surface microsculpture are used to identify genera and species, whereas colony morphology is useful at the family level. A molecular phylogeny by Waeschenbach et al. (2012) showed phylactolaemates to be the basal group in the phylum Bryozoa.

24.2 Bryozoan Studies in Japan

Japanese bryozoan diversity has been studied for well over a century. The earliest collection of Japanese marine bryozoans was made by the H.M.S. *Challenger* in 1873–1876 and described in the report on the expedition (Busk 1884). The first major report on the Japanese marine bryozoan fauna was Ortmann's (1890) monograph of a collection from Sagami Bay. Sagami Bay on the central Pacific Coast of Honshu Island is perceived as having an exceptionally diverse benthic fauna, including bryozoans. In the late nineteenth and early twentieth centuries, several researchers contributed to documenting this diversity, including Edward S. Morse, Ludwig H.P. Döderlein, and Franz T. Doflein (Isono 1988; National Science Museum Tokyo 2007). Döderlein collected various marine animals in Sagami Bay in 1880–1881, after he had finished his contract as a foreign advisory teacher in the Department of Medicine at Tokyo University, and noted a remarkably high diversity of bryozoans (Döderlein 1883). Ortmann (1890) worked on Döderlein's bryozoan collection, describing 159 species in total, including 84 new species; many of the original descriptions in this monograph form the basis for subsequent studies of marine bryozoans in Japan. Some of the specimens have been restudied (Mawatari and Suwa 1998; Hirose 2012a), but most have not been reexamined since Ortman (1890). In 1904–1905, the German zoologist Franz Doflein surveyed deep-sea animals in Sagami Bay. Doflein's collections contain numerous type specimens of Japanese deep-sea animals, but only a few of the many bryozoan specimens had been studied (Buchner 1924; Borg 1933), because of the large amount of material and the high species diversity involved.

Interest in Sagami Bay by Emperor Showa Hirohito between 1918 and 1971 resulted in considerable effort both in collecting in Sagami Bay and in curation of the collections, which include a large number of bryozoan specimens, most of which had not been studied until the recent revisional study by Hirose (2010). From 2001 to 2009, the National Science Museum Tokyo also conducted faunal surveys in Sagami Bay and collected additional specimens. Grischenko and Mawatari (2006) made a preliminary study of part of this material, collected in 2001–2003.

From early in the twentieth century to the present, researchers within and outside Japan have contributed to the knowledge of bryozoan diversity in Japanese waters (Okada 1917, 1920, 1921, 1923, 1925, 1928, 1929, 1934; Yanagi and Okada 1918; Canu and Bassler 1929; Harmer 1934, 1957; Sakakura 1935; Okada and Mawatari 1935, 1936, 1937, 1938; Silén 1941, 1942, 1947; S. Mawatari 1948, 1952, 1955, 1956, 1957, 1962, SF Mawatari 1971, 1972, 1986, 1987, 1988; Hayami 1973; Mawatari and Mawatari 1973c, 1974, 1981b; Kubota and Mawatari 1985a, b; d'Hondt and Mawatari 1986; Mawatari et al. 1988; Suwa and Mawatari 1998; Gordon et al. 2002; Grischenko et al. 2007). Shizuo Mawatari and his son, Shunsuke F. Mawatari, worked extensively on the taxonomy of anascan cheilostomes and produced a series of detailed publications (Mawatari 1973a, b, 1974; Mawatari and Mawatari 1979, 1980, 1981a, 1984, 1986a, b).

Freshwater bryozoans have been studied perhaps even more intensely than marine bryozoans in Japan. The earliest reports (Oka 1891, 1908a) involved the description of the common phylactolaemate species *Pectinatella gelatinosa* and *Stephanella hina* from Tokyo, followed by many reports on development and taxonomy (Oka 1891, 1907, 1908; Mukai and Oda 1980a, b; Oda and Mukai 1989; Mukai et al. 1990; Mukai 1999). Perhaps the most prolific researcher on phylactolaemates in Japan was Makoto Toriumi, who published on taxonomy, distribution, and intraspecific variation, with a focus on the Tohoku area (Toriumi 1941, 1942, 1943, 1944, 1951, 1952a, b, c, d, 1954a, b, 1955a, b, c, d, e, f, 1956a, b, c). There have been many other reports on the occurrence and distribution of phylactolaemates in Japan (Annandale 1922; Mawatari 1973c; Hirose 2012b; Hirose and Mawatari 2011a, b).

24.3 Bryozoan Diversity in Japan

For any group, the reported number of species in an area depends on research effort, including both the number of researchers and the sampling effort. Bryozoan colonies are easily overlooked and difficult for non-specialists to identify, and specimens reported in ecological studies were often not retained. Even in well-collected areas such as Sagami Bay, many specimens in collections have not been studied since their original descriptions, which are often inadequate and need reexamination in light of current taxonomy and using scanning electron microscope (SEM) images. In the past few decades, bryozoan diversity in Japan has begun to be reexamined in this way, and studies in previously investigated areas are adding new records for Japan. In this section, I review the current state of knowledge of bryozoan diversity in Japan based on published and unpublished records.

24.3.1 Freshwater and Brackish-Water Bryozoans

The taxonomy of phylactolaemates depends heavily on characters of statoblast microsculpture, which requires SEM observation, and several recent revisional studies have used SEM to examine phylactolaemate diversity in Japan (Wood 2001; Hirose and Mawatari 2011a, b). Freshwater ctenostomes have been poorly studied in Japan, although there has been one recent study based on the histological observation of internal morphology (Hirose and Mawatari 2011b). To date, 23 phylactolaemates in six families and three ctenostomes in three families have been reported from Japan (Table 24.1, Fig. 24.2), including new records and four recently described new species (Hirose and Mawatari 2011a, b).

Other studies investigating phylactolaemate phylogeny using morphological or molecular data have detected new genera. Oda and Mukai (1989) established the genus *Asajirella* based on the surface structure of statoblast valves and histological characters of the zooid epidermis. Based on molecular phylogeny, Hirose and Mawatari (2011a) established *Rumarcanella*, which was also corroborated by morphological characters such as hyper-tubercles on the floatoblast fenestra and the lack of vesicular pigments in the epidermis. The distributions of all 26 freshwater bryozoan species in Japan are listed in Table 24.1, based on published information and specimen records. Kyushu (southwestern Japan) and the Hokuriku area (coastal west-central Japan) have not been adequately surveyed, and studies in these areas might detect additional species.

The phylactolaemate diversity in Japan is marginally greater than that in North America or Europe, where about 20 and 17 species have been reported, respectively (Wood 1989; Wood and Okamura 2005). The family Plumatellidae shows higher diversity in Japan (15 species) than in North America (13) and Europe (10). Waterfowl use lakes and ponds on several migration routes through Japan, and the high plumatellid diversity might be related to statoblast dispersal by waterfowl (Hirose and Mawatari 2011a).

The Japanese phylactolaemate fauna contains both southern and northern elements. Most of the southern species such as *Asajirella gelatinosa*, *Plumatella javanica*, and *Rumarcanella vorstmani* also occur in Southeast Asia, whereas northern species such as *Cristatella mucedo* and *Plumatella fruticosa* occur in Europe and North America. Species having broad latitudinal ranges across several climatic zones, and the abundance of freshwater habitats of various sizes, have also probably contributed to the high diversity of phylactolaemates in Japan.

A common phylactolaemate throughout Hokkaido and Honshu is *Stephanella hina*, the sole extant species representing *Stephanella* and Stephanellidae.

Table 24.1 List of Japanese freshwater bryozoans

Class Order Family Genus	Species	Distribution
Phylactolaemata		
Plumatellida		
Plumatellidae		
Plumatella	*Plumatella repens* (Linnaeus, 1758)	HK, TH, KT, CB, KS, CG, SK, KY, OK
	Plumatella casmiana Oka, 1907	HK, TH, KT, CB, KS, SK, OK
	Plumatella emarginata Allman, 1844	HK, TH, KT, CB, KS, CG, SK, KY, OK
	Plumatella fungosa Pallas, 1768	KT, KS
	Plumatella mukaii Wood, 2001	HK, TH, KT, KS, OK
	Plumatella javanica Kraepelin, 1906	KT, SK, OK
	Plumatella rugosa (Wood, Wood, Geimer & Massard, 1998)	HK, TH, KT, KS, SK, KY
	Plumatella fruticosa Allman, 1844	HK, TH, KT, KS, CG, SK, KY
	Plumatella reticulata Wood, 1988	CG
Rumarcanella	*Rumarcanella vorstmani* (Toriumi, 1952)	TH, KT, KS, SK, KY, OK
	Rumarcanella minuta (Toriumi, 1941)	HK, TH, KT, CB, KS, SK, KY, OK
	Rumarcanella gusuku Hirose & Mawatari, 2011	OK
	Rumarcanella yanbaruensis Hirose & Mawatari, 2011	OK
Hyalinella	*Hyalinella punctata* (Hancock, 1850)	HK, TH, KT, CB, KS, CG, SK
Gelatinella	*Gelatinella toanensis* (Hozawa & Toriumi, 1940)	HK, TH, KT, KS, SK
Fredericellidae		
Fredericella	*Fredericella indica* Annandale, 1909	TH, KS
	Fredericella sultana (Blumenbach, 1779)	HK, TH, KT, CB, KS, SK, CG, KY
	Fredericella toriumii Hirose & Mawatari, 2011	KS
Pectinatellidae		
Pectinatella	*Pectinatella magnifica* (Leidy, 1851)	HK, TH, KT, KS, CG, SK, KY
Cristatellidae		
Cristatella	*Cristatella mucedo* Cuvier, 1798	HK, TH, KT
Lophopodidae		
Lophopodella	*Lophopodella carteri* (Hyatt, 1866)	HK, TH, KT, CB, KS, SK, KY, OK
Asajirella	*Asajirella gelatinosa* (Oka, 1891)	TH, KT, KS, SK

(continued)

Table 24.1 (continued)

Class Order Family Genus	Species	Distribution
Stephanellidae		
Stephanella	*Stephanella hina* Oka, 1908	HK, TH, KT, CB, KS, CG, SK
Gymnolaemata Ctenostomata Paludicellidae		
Paludicella	*Paludicella articulata* (Ehrenberg, 1831)	HK, TH, KT, KS, KY
Hislopiidae		
Hislopia	*Hislopia prolixa* Hirose & Mawatari, 2011	TH, KT, KS, KY
Victorellidae		
Victorella	*Victorella pavida* Saville Kent, 1870	HK, TH, KT, SK, KY

Appendix in distribution column: *HK* Hokkaido, *TH* Tohoku, *KT* Kanto, *CB* Chubu, *KS* Kansai, *CG* Chugoku, *SK* Shikoku, *KY* Kyushu, *OK* Okinawa

Molecular phylogeny (Okuyama et al. 2006; Hirose et al. 2008) has indicated it to be basal in Phylactolaemata. Uniquely among phylactolaemates in Japan, *Stephanella hina* forms colonies during winter, although details of its reproduction and development remain unknown.

The brackish-water bryozoan fauna has hardly been studied in Japan. Toriumi (1944) reported two ctenostomes and one cheilostome from a brackish habitat in Matsushima Bay, Miyagi Prefecture. Grischenko et al. (2007) listed 15 cheilostome species representing 12 genera, including *Cauloramphus*, *Electra*, *Pacificincola*, and *Microporella*, from Lake Akkeshi, connecting Akkeshi Bay with a narrow channel, in Hokkaido. A recent study on various brackish habitats in Japan detected several species of *Amathia* and *Microporella* in brackish lakes and inner bays on Hokkaido and Honshu.

24.3.2 Marine Bryozoans

Generally, marine bryozoans mostly have an encrusting colony form; however, the form varies according to the species (Fig. 24.3). Bryozoan colony form can strongly relate to habitat, environment, and ecology: flexible, erect colonies on various unstable substrata (Fig. 24.3a, e, j), robust branching or fenestrate colonies on hard substrata (Fig. 24.3b, c, d), rooted-erect or free-living colonies on soft bottoms (Fig. 24.3f, g, h, i), and small colonies occurring as epibionts on other organisms (Fig. 24.3k). Because of the high diversity in colony morphology and the variety of

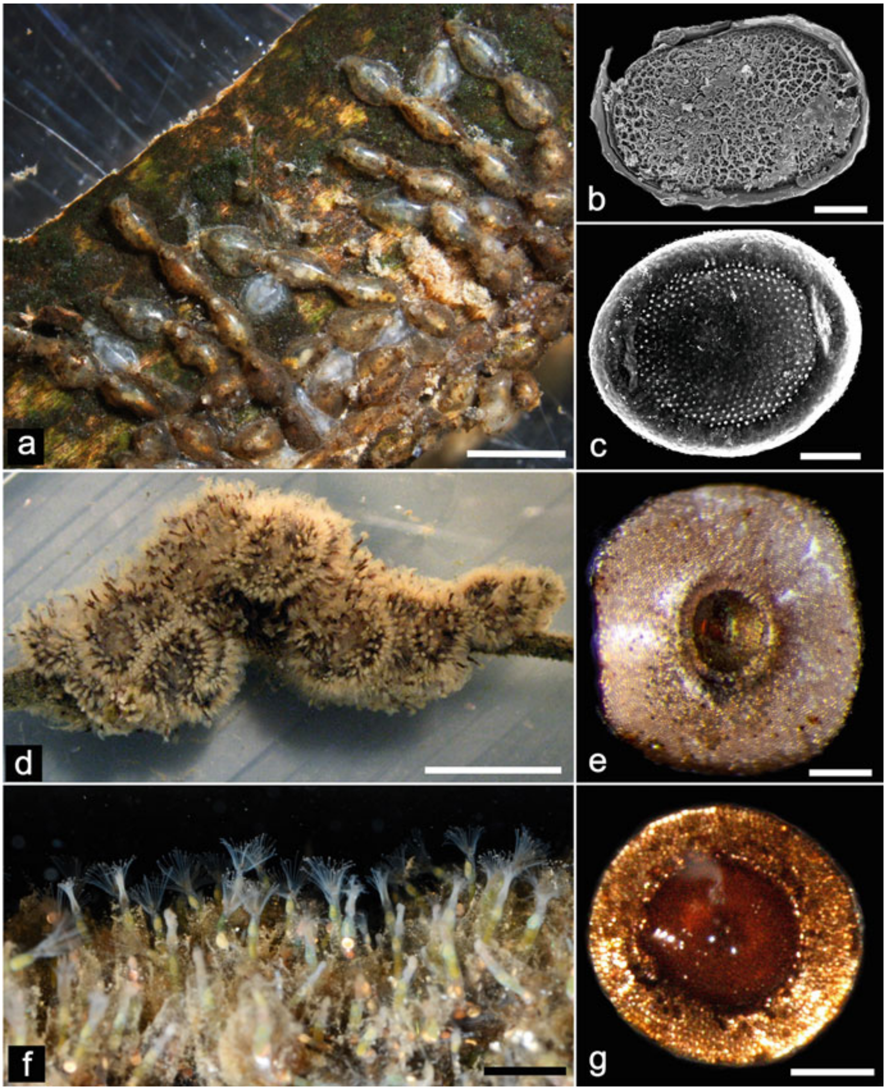

Fig. 24.2 Some Japanese freshwater bryozoans. **a** *Hislopia prolixa*. **b** Scanning electron micrograph (SEM) image of sessoblast of *Plumatella reticulata*. **c** SEM image of floatoblast of *Rumarcanella minuta*. **d** Colony of *Asajirella gelatinosa*. **e** Statoblast of *Asajirella gelatinosa*. **f** Colony of *Stephanella hina*. **g** Floatoblast of *Stephanella hina*. **a** Ctenostomata, **b**–**g** Phylactolaemata. *Bars* **a** 1 mm, **b** 100 μm, **c** 50 μm, **d** 2 cm, **e** 300 μm, **f** 3 mm, **g** 100 μm

environments occupied, an intensive survey is required for fully describing the Japanese marine bryozoan fauna.

The strong, warm Kuroshio Current and the cold Oyashio Current meet along the Pacific Coast of Japan, and both the currents and their associated thermal gradients

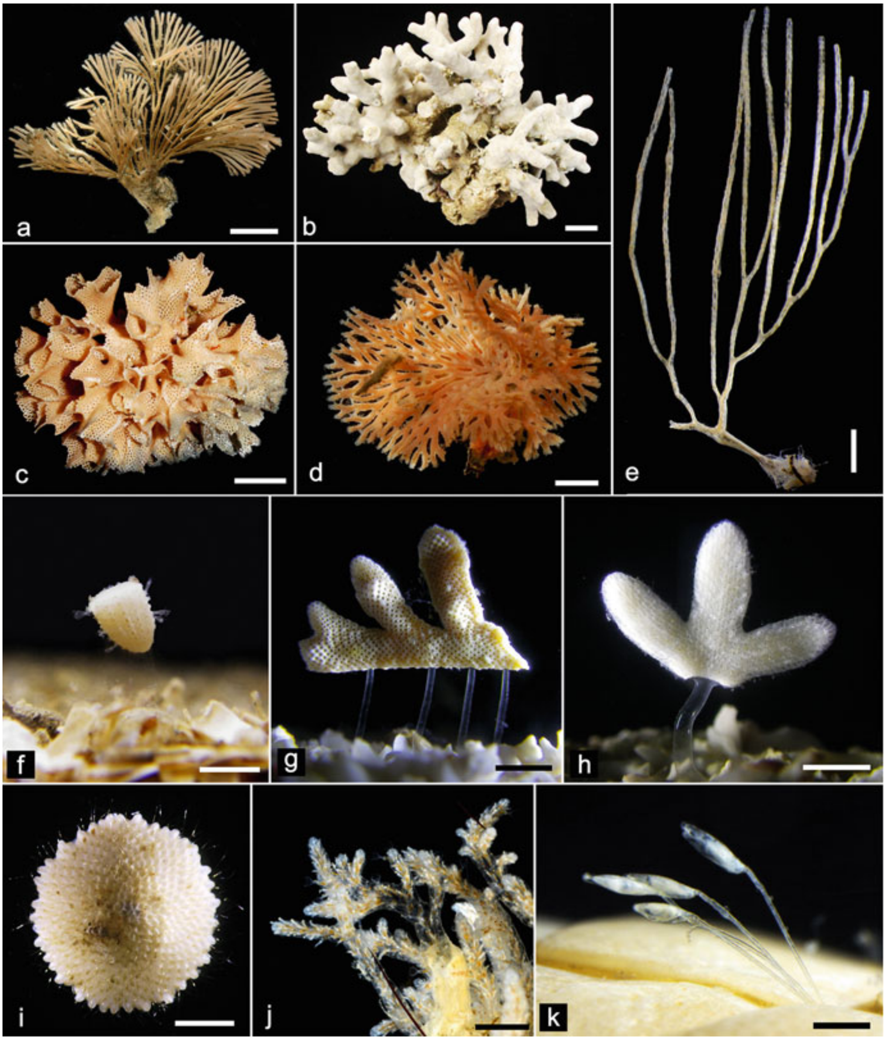

Fig. 24.3 Some colony forms in marine bryozoans from Japan. **a** *Caberea* (Cheilostomata, Candidae) from Tateyama (60 m). **b** *Heteropora* (Cyclostomata, Heteroporidae) from Otsuchi Bay (90 m). **c** *Triphyllozoon* (Cheilostomata, Phidoloporidae) from Okinawa (46 m). **d** *Reteporella* (Cheilostomata, Phidoloporidae) from Misaki, Sagami Bay (1 m). **e** *Columnella* (Cheilostomata, Farciminariidae) from Ogasawara (3600 m). **f** *Conescharellina* (Cheilostomata, Conescharellinidae) from the Nansei Islands (200 m). **g** *Flabellopora* (Cheilostomata, Conescharellinidae) from Okinawa (46 m). **h** *Lanceopora* (Cheilostomata, Lanceoporidae) from Koshiki Strait, Kyushu (83 m). **i** *Cupuladria* (Cheilostomata, Cupuladriidae) from Okinawa (15 m). **j** *Bockiella* (Ctenostomata, Alcyonidiidae) from off Sendai, Tohoku (190 m). **k** *Triticella* (Ctenostomata, Triticellidae) on *Bathynomus doederleinii* (Isopoda) from the Kumano Sea, off the Kii Peninsula (300 m). *Bars* **a**, **b**, **g** 1 cm, **c** 2 cm, **d**, **e**, **i**, **k** 5 mm, **e**, **j** 2 mm, **h** 3 mm

may affect the diversity and distribution of bryozoans in the region. Okada and Mawatari (1958) compared bryozoan diversity among several Indo-Pacific areas, such as the Malayan and Papuan Provinces; they speculated that northern and southern faunas meet on the Pacific Coast of central Japan around the 22 °C isotherm, the northern limit of the southern elements. Furthermore, as exemplified by Sagami Bay, the Pacific Coast of Japan is rich in bottom habitats, with depths reaching more than 1000 m close to shore. The Japanese bryozoan fauna has been best studied in nearshore shelf habitats, but less so intertidally, on sandy bottoms, and in deep water. Previously, Japanese bryozoan diversity had been estimated to be 300–1000 species (Scholz et al. 2008). Currently, however, approximately 500 species of marine bryozoans are known from the Japanese waters, and many habitats remain uninvestigated. Therefore, the diversity of Japanese marine bryozoans is likely much higher than presently documented, and may exceed 1000 species.

In a review of all the bryozoan collections made by Döderlein, Doflein, and Emperor Showa, and by the National Science Museum Tokyo from 2001 to 2005, Hirose (2010) tabulated around 260 cheilostome bryozoan species collected in Sagami Bay during the past 130 years. Figure 24.4 shows the number of species for 100-m depth intervals; the highest diversity occurs in the upper 200 m, as reported for other regions, such as New Zealand (Gordon 1999). The eastern side of Sagami Bay shows a higher diversity of bryozoan species, which is perhaps partly related to the greater number of specimens from that area, but also to the variety of bottom environments, including several submarine canyons and knolls. The bryozoan fauna of Sagami Bay is characterized by a high diversity of fenestrate phidoloporid species. In Sagami Bay and the Sagami Sea, some other families

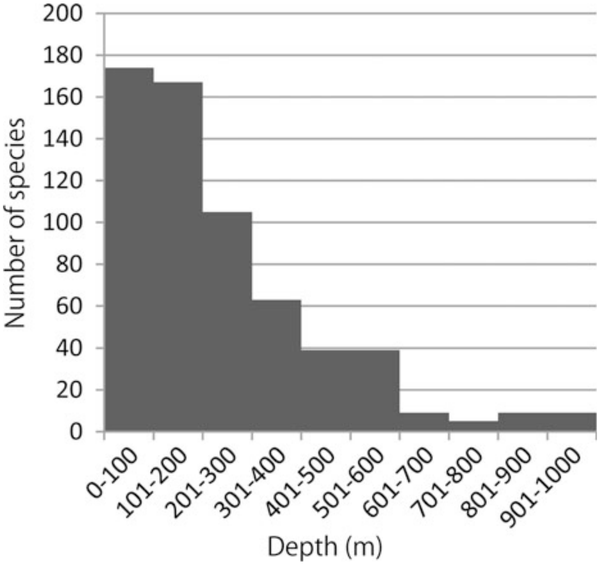

Fig. 24.4 Number of cheilostome bryozoan species with depth in Sagami Bay, at 100-m intervals

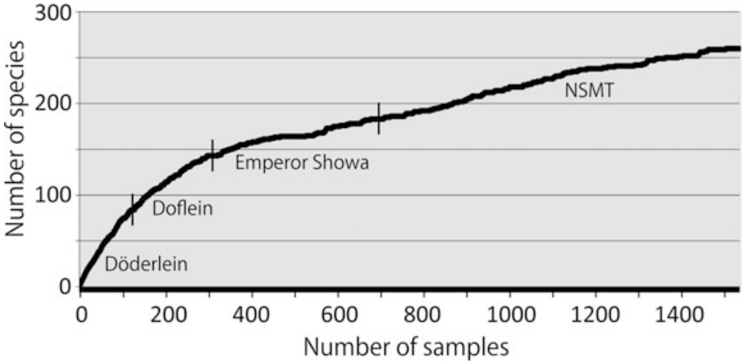

Fig. 24.5 Species accumulation curve for cheilostome bryozoans in the Sagami Bay collected across 130 years. *Vertical bars* on the curve indicate the border of collections made by Döderlein, Doflein, Emperor Showa, and the National Science Museum Tokyo (NSMT)

such as Smittinidae, Calloporidae, Candidae, Celleporidae, and Lepraliellidae are also speciose. Although more than 1000 specimens from Sagami Bay were recently examined (Hirose 2010, 2012a), the species accumulation curve (Fig. 24.5) has not leveled off, suggesting more species will be detected.

Table 24.2 lists by area the number of genera and species of marine bryozoans reported from Japan in the literature, starting with Ortmann (1890). With the apparent exception of the Kii Peninsula, the areas with the highest known diversity (Hokkaido and Sagami Sea) are the areas with the highest research effort in the number of publications. An exceptionally high diversity of bryozoans, based on fewer publications, in the Kii Peninsula resulted from the large revisionary reports on the local fauna. Bryozoan faunas in other areas such as Kyushu, Shikoku, and the Seto Inland Sea have hardly been studied in detail but only mentioned as examined specimens from some areas in several reports (Table 24.2).

In the first review of cyclostomes around Japan, Okada (1917) reported 32 species representing 7 genera from Sagami Sea, Hokkaido, and Kagoshima. Mawatari (1955) listed 78 species in 23 genera from Japanese waters, including fossil records, and Mawatari and Mawatari (1973c, 1974) reported 31 species representing 14 genera from Hokkaido.

Cheilostomes are the most diverse bryozoan group in Recent seas, 7.4 and 10.5 times as diverse as cyclostomes around New Zealand and Australia, respectively (Gordon 1999). Mawatari (1952) reported 129 species of cheilostomes around Kii Peninsula. Silén (1941) examined bryozoan specimens collected from Ogasawara and some other localities by S. Bock, T. Gislén, and the *Vega* Expedition, and reported 88 species of anascan cheilostomes, representing 47 genera. Mawatari and Mawatari (1981b) listed 130 species, representing 63 genera, in a review of the cheilostomes around Hokkaido. They also reported 112 species of anascans, representing 40 genera, from Japan in a series of publications (Mawatari 1973a, b, 1974; Mawatari and Mawatari 1979, 1980, 1981a, 1984, 1986a, b). Cheilostomes, however, were only three and six times as speciose as cyclostomes in Sagami Bay

Table 24.2 Number of genera and species of Japanese marine bryozoans reported in references

Area	Publication	Maximum depth (m)	Ctenostomata		Cheilostomata		Cyclostomata	
			Genera	Species	Genera	Species	Genera	Species
Hokkaido (and Kurile Islands)								
1	Borg (1933)	67					1	1
2	Mawatari (1956)[a]	–			25	32		
3	Mawatari (1957)	–			2	2		
4	Mawatari (1971)	–	1	3				
5	Mawatari (1972)	–	1	1				
6	Mawatari and Mawatari (1973c)[a]	–					3	10
7	Mawatari and Mawatari (1974)[a]	–					11	21
8	Mawatari and Mawatari (1981b)[a]	–			63	130		
9	Mawatari (1986)	–			1	1		
10	d'Hondt and Mawatari (1986)[b]	19	1	6				
11	Kubota and Mawatari (1985a)[b]	2			6	6		
12	Kubota and Mawatari (1985b)[b]	2			4	4		
13	Mawatari et al. (1988)	–			8	8		
14	Mawatari (1988)[b]	22			2	2		
15	Suwa and Mawatari (1998)[b]	27			1	7		
16	Ikezawa and Mawatari (1993)	0.5			1	3		
17	Grischenkko et al. (2007)[ab]	Intertidal			26	39		
			3	**10**	**78**	**185**	**14**	**31**
Tohoku (NE Japan), Pacific coast								
1	Okada (1928)[a]	–					5	12
2	Okada (1929)[a]	–			18	27		
3	Okada and Mawatari (1937)[a]	39			14	16	3	3
4	Mawatari (1948)[a]	–	5	6	21	24	3	4
5	d'Hondt and Mawatari (1986)[b]	19	1	1				
			5	**7**	**32**	**51**	**6**	**19**

Tohoku (NE Japan), Sea of Japan								
1	Mawatari and Mawatari (1979)	–			5	5		
2	Mawatari and Mawatari (1980)	–			1	1		
3	Hayami (1973)[a]	210			17	21		
					23	**27**		
Sagami Bay/Sea, Tokyo Bay								
1	Ortmann (1890)[a]	457			34	100	9	28
2	Okada (1917)	731					7	32
3	Yanagi and Okada (1918)	640			7	28		
4	Okada (1920)	570			2	14		
5	Okada (1921)	530			6	6		
6	Buchner (1924)	600			2	18		
7	Borg (1933)	185					1	1
8	Okada (1934)[a]	–			20	22		
9	Okada and Mawatari (1935)[a]	130			18	20	5	7
10	Okada and Mawatari (1936)[a]	–			17	24		
11	Silén (1942)[ab]	600	3	7				
12	Silén (1947)	300			2	2		
13	Mawatari (1953)	128	2	4				
			4	**10**	**59**	**179**	**15**	**59**
Ogasawara (Bonin Islands)								
1	Silén (1941)[ab]	600			47	88		
2	Silén (1942)[ab]	135	3	4				
3	Okada (1917)	82					1	1
			3	**4**	**50**	**94**	**1**	**1**
Kii Peninsula (Pacific Coast, middle Honshu)								
1	Okada and Mawatari (1938)[a]	–	1	1	38	59	5	8
2	Mawatari (1952)[a]	–	4	5	78	129	7	15
			4	**4**	**76**	**144**	**6**	**17**

(continued)

Table 24.2 (continued)

Area	Publication	Maximum depth (m)	Ctenostomata		Cheilostomata		Cyclostomata	
			Genera	Species	Genera	Species	Genera	Species
Noto Peninsula (Sea of Japan, middle Honshu)								
1	Mawatari (1962)[a]	–	3	4	55	70	5	7
2	Mawatari (1964)	–			1	1		
3	Sakakura (1935)[a]	274			24	33	4	7
			3	**4**	**65**	**92**	**7**	**11**
Shikoku (Pacific Coast)								
1	Ortmann (1890)	–			1	1		
2	Mawatari (1955)	–					1	2
3	Okada and Mawatari (1938)	–			1	1		
4	Mawatari (1974)	–			1	1		
5	Mawatari and Mawatari (1979)	–			1	1		
6	Mawatari and Mawatari (1986b)	15			1	1		
					4	**4**	**1**	**2**
Seto Inland Sea								
1	Yanagi and Okada (1918)	–			2	2		
2	Okada (1920)	–			1	1		
3	Okada (1934)	–			8	8		
4	Okada and Mawatari (1938)	–			7	7		
5	Mawatari (1973a)	–			1	2		
6	Mawatari (1974)	–			1	1		
					13	**14**		
Korea Strait (between East China Sea and Sea of Japan)								
1	Okada (1923)[a]	200			21	40	5	9
2	Okada (1925)	119	1	1				
			1	**1**	**21**	**40**	**5**	**9**

Kyushu (East China Sea and southern part)								
1	Ortmann (1890)	91			1	1		
2	Mawatari (1955)	128					2	4
3	Okada (1917)	128					2	2
4	Okada (1921)	99			1	1		
5	Okada (1920)	99			2	2		
6	Okada (1934)	–			4	4		
7	Okada and Mawatari (1938)	–			4	4	1	1
8	Silen (1941)[b]	300			20	31		
9	Silen (1942)[b]	135	6	7				
10	Silen (1947)	175			3	6		
11	Mawatari (1973a)	–			1	3		
12	Mawatari (1973b)	–			2	2		
13	Mawatari (1974)	–			3	4		
14	Mawatari and Mawatari (1980)	120			3	5		
15	Mawatari and Mawatari (1981a)	–			2	2		
16	Mawatari and Mawatari (1984)	300			2	2		
17	Mawatari and Mawatari (1986b)	30			1	1		
			6	**7**	**39**	**63**	**2**	**5**
Nansei Islands (including Okinawa)								
1	Okada (1920)	–			1	1		
2	Okada (1934)	–			2	2		
3	Mawatari and Mawatari (1984)	35			1	1		
4	Mawatari (1987)[a]	10			21	22		
					24	**26**		

Numbers in *bold* characters indicate the total number of the genera or species in each region

[a] Revisional study on the local fauna in the area

[b] Including intertidal locality

and around Hokkaido, respectively (Table 24.2); therefore, cheilostome bryozoan diversity is probably higher than currently reported in these areas, or cyclostome diversity in the area is greater than in Australia/New Zealand.

In general, ctenostome diversity is poorly known because identification is difficult, being often based on internal morphology, and there are few specialists who study ctenostomes; only 37 species, representing 15 genera, have been reported from Japanese waters (Okada 1925; Okada and Mawatari 1938; Silén 1942; S. Mawatari 1948, 1952, 1953, 1962, 1964; S.F. Mawatari 1971, 1972; d'Hondt and Mawatari 1986, 1987).

The maximum depth reported for each study in Table 24.2 shows a bias in depths surveyed among areas; for example, several studies examined specimens from deeper than 500 m in the Sagami Sea, whereas the maximum depth reported for specimens around Hokkaido is 67 m. There are only a single report of bryozoans collected at depths more than 1000 m in Japanese waters (d'Hondt and Mawatari 1987). The intertidal bryozoan fauna has also been relatively poorly studied; a recent intertidal study (Grischenko et al. 2007) reported 9 new species (23 %) and 21 new species records (54 %) for Japan, among 39 cheilostome species detected at ten sampling sites in Akkeshi Bay, Hokkaido. In fact, in the past two decades, intensive studies of local bryozoan faunas at a variety of depths and in various parts of the world have detected 20–40 % new species (Grischenko et al. 2007). A recent study (Dick and Grischenko, unpublished data) on intertidal bryozoans in the Sesoko area, Okinawa, yielded 52 cheilostome species, representing 34 genera, at three sampling sites; most of the species (~87 %) are either new species or new records for Japan. Thus, it is reasonable to assume that knowledge of the bryozoan fauna of Japan is far from complete from all habitats and depths, but particularly from deep shelf habitats.

An assessment of bryozoan diversity in Japan will also require intensive local studies at many sites throughout the country; high local sampling effort is necessary to detect uncommon species, and a high density of study sites is necessary to detect an unknown proportion of marine bryozoan species that have rather limited ranges, on the order of hundreds rather than thousands of kilometers. In a recent survey at Otsuchi (a previously uninvestigated locality in Tohoku), I detected at least 53 species representing 44 genera, a greater diversity than at any other previously reported locality in Tohoku. A large collection made in a recent survey by several research vessels in the southwestern region (Nansei Islands) contains more than 130 species in 70 genera, including many new records for Japan. As noted by Okada and Mawatari (1958), the bryozoan fauna is largely different between the northwestern and southwestern Pacific; Otsuchi Bay has many genera in common with Hokkaido and the Kuril Islands (e.g., *Celleporella* and *Heteropora*), whereas in Okinawa there are typical genera (e.g., *Cellaria*, *Lanceopora* and *Iodictyum*) in common with the Philippines.

Bryozoan faunas also differ with depth and bottom environment, and inventories should take this into account. In a recent dredging survey at the vicinity of Akkeshi, Hokkaido, I detected 59 species representing 43 genera at depths from 8.5 to 129 m. Only 8 of these species (13.5 %) were also reported intertidally by Grischenko et al. (2007) (*Tegella aquilirostris*, *Callopora craticula*, *Parkermavella orientalis*, *Phidolopora elongata*, *Celleporina minima*, *Myriozoella plana*, *Fenestrulina orientalis*, *Porella belli*). Recent sampling in sandy-bottom habitats around Japan has also revealed a previously undetected high diversity of sand-dwelling species such as Conescharellinidae and *Lanceopora* (Fig. 24.3h, i). In a recent survey of sand-dwelling bryozoans around Japan, at least 25 species representing 8 genera were detected from Okinawa to Tohoku (Hirose, unpublished data). Finally, only recently have bryozoans been collected from the 1000 to 3600 m depth interval around Japan, with several erect cheilostome species obtained from the Nansei and Bonin Islands.

Bryozoan colonies have many ecological functions in benthic habitats throughout the fossil record to the present day; bryozoan colonies provide a habitat for other organisms, and their fragments also contribute to marine carbonate sediments and derivative limestones. Therefore, further study of the taxonomy and diversity of Recent bryozoans will advance knowledge of the systematics, marine ecology, paleoecology, and evolution of the sessile fauna of Japanese waters.

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References

Annandale N (1922) The macroscopic fauna of Lake Biwa. Ann Zool Jpn 10:127–153

Bock PE, Gordon DP (2013) Phylum Bryozoa Ehrenberg, 1831. In: Zhang Z-Q (ed) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness (Addenda 2013), Zootaxa 3703. Magnolia Press, Oakland, pp 67–74

Borg F (1933) A revision of the recent Heteroporidae (Bryozoa). Zool Bidr Uppsala 14:253–294

Buchner P (1924) Studien über den Polymorphismus der Bryozoen. 1. Anatomisch und systematische Untersuchungen an japanischen Reteporiden. Zool Jb Syst Geogr Biol 48:155–216

Busk G (1884) Report on the Polyzoa collected by H.M.S. Challenger during the years 1873–1876. Part 1. The Cheilostomata. In: Wyville Thomson C, Murray J (eds) Report on the scientific results of the voyage of H.M.S. challenger, zoology part XXX, vol 10. Her Majesty's Government, London, pp 1–216

Canu F, Bassler RS (1929) Bryozoa of the Philippine region. US Natl Mus Bull 100:1–685

d'Hondt J-L, Mawatari SF (1986) Les *Alcyonidium* (Bryozoa, Ctenostomida) des côtes du Japon. Bull Mus Natl Hist Nat 8:457–469

d'Hondt J-L, Mawatari SF (1987) Description de deux nouvelles espèces d'Arachnoidea (Bryozoa, Ctenostomida) provenant de la campagen océanographique KAIKO I (Japon). Cah Biol Mar 28:373–380

Döderlein LHP (1883) Faunistische Studien in japan: Enoshima und die Sagami-Bai. Arch Naturgesch 49:102–123

Gordon DP (1999) Bryozoan diversity in New Zealand and Australia. In: Ponder W, Lunney D (eds) The other 99%. The conservation and biodiversity of invertebrates. Transactions of the Royal Zoological Society of New South Wales, Mosman, pp 199–204

Gordon DP (2000) A thousand, two hundred, or fifty more years? Can we shorten the time to biodiversity inventory? Pac World 57:39–43

Gordon DP, Mawatari SF, Kajihara H (2002) New taxa of Japanese and New Zealand Eurystomellidae (Phylum Bryozoa) and their phylogenetic relationships. Zool J Linn Soc 136:199–216

Grischenko AV, Mawatari SF (2006) On the bryozoan diversity of Sagami Bay. Mem Nat Sci Mus Tokyo 40:187–201

Grischenko AV, Dick MH, Mawatari SF (2007) Diversity and taxonomy of intertidal Bryozoa (Cheilostomata) at Akkeshi Bay, Hokkaido, Japan. J Nat Hist 41:1047–1161

Harmer SF (1934) The Polyzoa of the Siboga expedition. Part 3. Cheilostomata Ascophora, I. Family Reteporidae. Siboga Exped Rep 28c:502–640

Harmer SF (1957) The Polyzoa of the Siboga expedition, Part 4. Cheilostomata Ascophora II. Siboga Exped Rep 28d:641–1147

Hayami T (1973) The recent Cheilostomata (Bryozoa) from Kuroko-Shima, Northern Honshu, Japan. Saito Ho-on Kai Mus Res Bull 42:47–56

Hirose M (2010) Cheilostomatous Bryozoa (Gymnolaemata) from Sagami Bay, with notes on Bryozoan diversity and faunal changes over the past 130 years. Dissertation, Graduate School of Science, Hokkaido University

Hirose M (2012a) Revision of the genus *Buchneria* (Bryozoa, Cheilostomata) from Japan. ZooKeys 241:1–19

Hirose M (2012b) Taxonomy and identification of freshwater bryozoans from Japan. TAXA (Proc Jap Soc Syst Zool) 33:17–32 [in Japanese with English abstract]

Hirose M, Mawatari SF (2011a) Freshwater Bryozoa of Okinawa, Japan, with descriptions of *Rumarcanella* gen. nov. (Phylactolaemata: Plumatellidae) and two new species. Zootaxa 2732:1–19

Hirose M, Mawatari SF (2011b) Freshwater Bryozoa of Lake Biwa, Japan. Species Divers 16:1–37

Hirose M, Dick MH, Mawatari SF (2008) Molecular phylogenetic analysis of phylactolaemate bryozoans based on mitochondrial gene sequences. In: Hageman SJ, Key MM Jr, Winston JE (eds) Bryozoan studies 2007, Special Publication Number 15. Virginia Museum of Natural History, Martinsville, pp 65–74

Ikezawa H, Mawatari SF (1993) A systematic study of three species of Celleporina (Bryozoa, Cheilostomata) from Hokkaido, Japan with special reference to their early astogeny. Zool Sci 10:1029–1043

Isono N (1988) Personnels related to Misaki Marine Biological Laboratory: birth of zoology in Japan. Gakkai Shuppan Center, Tokyo [in Japanese]

Kubota K, Mawatari SF (1985a) A systematic study of Cheilostomatous Bryozoans from Oshoro Bay, Hokkaido. 1. Anasca. Environ Sci Hokkaido Univ 8:75–91

Kubota K, Mawatari SF (1985b) A systematic study of Cheilostomatous Bryozoans from Oshoro Bay, Hokkadio 2. Ascophora. Environ Sci Hokkaido Univ 8:195–208

Mawatari S (1948) Bryozoan fauna of Matsushima Bay, Northern Honshu, Japan (preliminary report). Proc Biogeogr Soc Jpn 2:1–5

Mawatari S (1952) Bryozoa of Kii Peninsula. Publ Seto Mar Biol Lab 2:261–288

Mawatari S (1953) Studies on Japanese ctenostomatous Bryozoa. I. On some species of Carnosa. Publ Seto Mar Biol Lab 3:213–220

Mawatari S (1955) A check list of known species of Japanese cyclostomatous Bryozoa. Bull Biogeogr Soc Jpn 16-19:44–50

Mawatari S (1956) Cheilostomatous Bryozoa from the Kurile Islands and the neighbouring districts. Pac Sci 10:113–135

Mawatari S (1957) On two bryozoans from Hokkaido. J Fac Sci Hokkaido Univ Ser VI Zool 13:78–84

Mawatari S (1962) Bryozoa of the eastern shore of Noto Peninsula. Ann Rep Noto Mar Lab/Noto Mar Lab Fac Sci Univ Kanazawa 3:5–10

Mawatari S (1964) On *Cothurnicella japonica* n. sp. Ann Rep Noto Mar Lab/Noto Mar Lab Fac Sci Univ Kanazawa 4:23–32

Mawatari SF (1971) Three species of *Flustrellidra* (Bryozoa, Ctenostomata) from Hokkaido. J Fac Sci Hokkaido Univ Ser VI Zool 18:227–234

Mawatari SF (1972) A new species of the genus *Bowerbanki*a (Bryozoa, Ctenostomata) from Hokkaido. J Fac Sci Hokkaido Univ Ser VI Zool 18:300–304

Mawatari S (1973a) Studies on Japanese Anascan Bryozoa. 1. Inovicellata. Bull Natl Sci Mus Tokyo 16:409–428

Mawatari S (1973b) Studies on Japanese anascan Bryozoa. 2. Division Scrupariina. Bull Natl Sci Mus Tokyo 16:605–624

Mawatari S (1973c) New occurrence of *Pectinatella magnifica* (Leidy) in a Japanese lake. Proc Jap Soc Syst Zool 9:41–43

Mawatari S (1974) Studies on Japanese Anascan Bryozoa. 3. Division Malacostega (1). Bull Natl Sci Mus Tokyo 17:17–52

Mawatari SF (1986) A new genus and species of celleporid bryozoan with ancestrular triad from Hokkaido, Japan. J Nat Hist 20:193–202

Mawatari SF (1987) A preliminary list of cheilostomatous bryozoans from Sesoko, Okinawa. Galaxea 6:99–107

Mawatari SF (1988) Two cheilostomatous bryozoans new to Hokkaido. Mem Nat Sci Mus Tokyo 21:145–151

Mawatari S, Mawatari SF (1973) Notes on the marine Bryozoa from Hokkaido. 1. Crisiidae (Cyclostomata). J Fac Sci Hokkaido Univ Ser VI Zool 19:95–104

Mawatari S, Mawatari SF (1974) Notes on the marine Bryozoa from Hokkaido. 2. Cyclostomata other than Crisiidae. J Fac Sci Hokkaido Univ Ser VI Zool 19:349–360

Mawatari S, Mawatari SF (1979) Studies on Japanese anascan Bryozoa. 4. Division Malacostega (2). Bull Lib Arts Sci Course Sch Med Nihon Univ 7:11–52

Mawatari S, Mawatari SF (1980) Studies on Japanese anascan Bryozoa 5. Division Malacostega (3). Bull Lib Arts Sci Course Sch Med Nihon Univ 8:21–114

Mawatari S, Mawatari SF (1981a) Studies on Japanese anascan Bryozoa. 6. Division Malacostega (4). Bull Lib Arts Sci Course Sch Med Nihon Univ 9:23–61

Mawatari SF, Mawatari S (1981b) A preliminary list of cheilostomatous bryozoans collected along the coasts of Hokkaido. Proc Jap Soc Syst Zool 21:41–58

Mawatari SF, Mawatari S (1984) Studies on Japanese anascan Bryozoa. 7. Division Malacostega (5). Environ Sci Hokkaido Univ 7:109–120

Mawatari SF, Mawatari S (1986a) Studies on Japanese anascan Bryozoa. 8. Division Malacostega (6). Environ Sci Hokkaido Univ 9:239–246

Mawatari SF, Mawatari S (1986b) Studies on Japanese anascan Bryozoa. 9. Division Malacostega (7). Environ Sci Hokkaido Univ 11:11–14

Mawatari SF, Suwa T (1998) Two new species of Japanese *Microporella* (Bryozoa, Cheilostomatida) in the Döderlein Collection, Musée Zoologique, Strasbourg. Cah Biol Mar 39:1–7

Mawatari SF, Kubota S, Konishi K, Sato T, Kuwahara Y, Yamada M (1988) A list of marine invertebrates collected around the Kikonai Marine Station. Seibutsu Kyozai 23:1–12 [in Japanese]

Mukai H (1999) Comparative morphological studies on the statoblasts of lower phylactolaemate bryozoans, with discussion on the systematics of the Phylactolaemata. Sci Rep Fac Educ Gunma Univ 46:51–91

Mukai H, Oda S (1980a) Histological and histochemical studies on the epidermal system of higher phylactolaemate bryozoans. Annot Zool Jpn 53:1–17

Mukai H, Oda S (1980b) Comparative studies on the statoblasts of higher phylactolaemate bryozoans. J Morphol 165:131–155

Mukai H, Backus BT, Wood TS (1990) Comparative studies of American, European and Japanese forms of *Plumatella emarginata*, a freshwater bryozoan. Proc Jap Soc Syst Zool 42:51–59

National Science Museum Tokyo (2007) Fauna Sagamiana. Tokai University Press, Tokyo [in Japanese]

Oda S, Mukai H (1989) Systematic position and biology of *Pectinatella gelatinosa* Oka (Bryozoa: Phylactolaemata) with the description of a new genus. Zool Sci 6:401–408

Oka A (1891) Observation on fresh-water Polyzoa (*Pectinatella gelatinosa*, nov. sp.). J Coll Sci Imp Univ Jpn 4:89–150

Oka A (1907) Zur Kenntnis der Süsswasser-Bryozoen fauna von Japan. Annot Zool Jpn 6:117–123

Oka A (1908) Ueber eine neue Gattung von Süsswasser bryozoen (*Stephanella* n. g.). Annot Zool Jpn 6:277–285

Okada Y (1917) A report on the cyclostomatous Bryozoa of Japan. Annot Zool Jpn 9:335–360

Okada Y (1920) Notes on some species of *Retepora* and *Adeonella* occurring in Japan, with descriptions of one new variety and five new species. Annot Zool Jpn 9:613–634

Okada Y (1921) Notes of some Japanese cheilostomatous Bryozoa. Annot Zool Jpn 10:19–32

Okada Y (1923) On a collection of Bryozoa from the Straits of Corea. Annot Zool Jpn 10:215–234

Okada Y (1925) *Alcyonidium* (*Paralcyonidium*) *vermiculare*, a new subgenus and species of ctenostomatous Bryozoa. Annot Zool Jpn 10:281–284

Okada Y (1928) Report of the biological survey of Mutsu Bay. 8. Cyclostomatous Bryozoa of Mutsu Bay. Sci Rep Tohokuk Imp Univ Fourth Ser Biol 3:481–496

Okada Y (1929) Report of the biological survey of Mutsu Bay. 12. Cheilostomatous Bryozoa of Mutsu Bay. Sci Rep Tohokuk Imp Univ Fourth Ser Biol 4:11–35

Okada Y (1934) Bryozoan fauna in the vicinity of the Shimoda Marine Biological Station. Sci Rep Tokyo Bunrika Daigaku Sect B 2(26):1–20

Okada Y, Mawatari S (1935) Bryozoa fauna collected by the ‘Misago’ during the zoological survey around Izu Peninsula (I). Sci Rep Tokyo Bunrika Daigaku Sect B 2(35):127–147

Okada Y, Mawatari S (1936) Bryozoa fauna collected by the ‘Misago’ during the zoological survey around Izu Peninsula (II). Sci Rep Tokyo Bunrika Daigaku Sect B 3(49):53–73

Okada Y, Mawatari S (1937) On the collection of Bryozoa along the coast of Onagawa Bay and its vicinity, the northern part of Honshu, Japan. Sci Rep Tohokuk Imp Univ Fourth Ser Biol 11:433–445

Okada Y, Mawatari S (1938) On the collection of Bryozoa along the coast of Wakayama-ken, the middle part of Honsyu, Japan. Annot Zool Jpn 17:445–463

Okada Y, Mawatari S (1958) Distributional provinces of marine Bryozoa in the Indo-Pacific region. Proceedings of the eighth Pacific Science Congress of the Pacific Science Association, vol 3. National Research Council of the Philippines, University of the Philippines, Quezon City, pp 391–402

Okuyama M, Wada H, Ishii T (2006) Phylogenetic relationships of freshwater bryozoans (Ectoprocta, Phylactolaemata) inferred from mitochondrial ribosomal DNA sequences. Zool Scr 35:243–249

Ortmann A (1890) Die Japanische Bryozoenfauna. Bericht über die von Herrn Dr. L. Döderlein in Jahre 1880–1881 gemachten Sammlungen. Arch Naturgeschafte 54(1):1–74

Ryland JS (2005) Bryozoa: an introductory overview. Denisia 16:9–20

Sakakura K (1935) Bryozoa from Toyama Bay, Sea of Japan. Annot Zool Jpn 15:106–118

Scholz J, Mawatari SF, Hirose M (2008) The Bryozoan diversity mystery: why do we have about 1,000 species in Japanese waters? In: Okada H, Mawatari SF, Suzuki N, Gautam P (eds) Origin and evolution of natural diversity. Proceedings of the International Symposium “The Origin and Evolution of Natural Diversity”, 21st century COE for neo-science of natural history. Hokkaido University, Sapporo, pp 129–135

Silén L (1941) Cheilostomata Anasca (Bryozoa) collected by Prof. Dr. Sixten Bock’s expedition to Japan and the Bonin Islands 1914. Arkh Zool 33A:1–130

Silén L (1942) Carnosa and Stolonifera (Bryozoa) collected by Prof. Sixten Bock’s expedition to Japan and the Bonin Islands 1914. Ark Zool 34A:1–33

Silén L (1947) Conescharellinidae (Bryozoa Gymnolaemata) collected by Prof. Dr. Sixten Bock’s expedition to Japan and the Bonin Islands 1914. Ark Zool 39A:1–59

Suwa T, Mawatari SF (1998) Revision of seven species of *Microporella* (Bryozoa, Cheilostomatida) from Hokkaido, Japan, using new taxonomic characters. J Nat Hist 32:895–922

Toriumi M (1941) Studies on freshwater Bryozoa of Japan. 1. Sci Rep Tohokuk Imp Univ Fourth Ser Biol 16:193–215

Toriumi M (1942) Studies on freshwater Bryozoa of Japan. 3. Freshwater Bryozoa of Hokkaido. Sci Rep Tohokuk Imp Univ Fourth Ser Biol 17:197–205

Toriumi M (1943) Studies on freshwater Bryozoa of Japan. 5. The variations occurring in the statoblasts and in the number of the tentacles of *Cristatella mucedo* Cuvier. Sci Rep Tohoku Imp Univ Fourth Ser Biol 17:247–253

Toriumi M (1944) About brackish bryozoa. Doubutsugaku Zasshi (Zool Mag) 56:20–25 [in Japanese]

Toriumi M (1951) Taxonomical study on freshwater Bryozoa. 1. *Fredericella sultana* (Blumenbach). Sci Rep Tôhoku Univ Fourth Ser Biol 19:167–177

Toriumi M (1952a) Taxonomical study on fresh-water Bryozoa. 2. *Paludicella articulate* (Ehrenberg). Sci Rep Tôhoku Univ Fourth Ser Biol 19:255–259

Toriumi M (1952b) Taxonomical study on fresh-water Bryozoa. 4. On *Plumatella javanica* Kraepelin reported by Vorstman in 1928. Sci Rep Tohoku Univ Fourth Ser Biol 19:264–269

Toriumi M (1952c) Taxonomical study on fresh-water Bryozoa. 5. On a geminate form named *Plumatella jugalis* by Allman. Sci Rep Tohoku Univ Fourth Ser Biol 19:315–319

Toriumi M (1952d) Taxonomical study on freshwater Bryozoa. 6. *Plumatella emarginata* Allman. Sci Rep Tohoku Imp Univ Fourth Ser Biol 19:320–334

Toriumi M (1954a) Taxonomical study on fresh-water Bryozoa. 7. Additions to the reconsideration on the ectocyst of *Plumatella emarginata* Allman. Sci Rep Tohoku Univ Fourth Ser Biol 20:287–293

Toriumi M (1954b) Taxonomical study on freshwater Bryozoa. 8. *Plumatella fruticosa* Allman. Sci Rep Tohoku Imp Univ Fourth Ser Biol 20:293–302

Toriumi M (1955a) Taxonomical study on freshwater Bryozoa. 9. *Plumatella repens* (L.). Sci Rep Tohoku Imp Univ Fourth Ser Biol 21:51–67

Toriumi M (1955b) Taxonomical study on fresh-water Bryozoa. 10. *Plumatella casmiana* Oka. Sci Rep Tohoku Univ Fourth Ser Biol 21:67–77

Toriumi M (1955c) Taxonomical study on freshwater Bryozoa. 11. *Stephanella hina* Oka. Sci Rep Tôhoku Univ Fourth Ser Biol 21:131–136

Toriumi M (1955d) Taxonomical study on freshwater Bryozoa. 12. On *Plumatella repens* var. *minuta* Toriumi, 1941. Sci Rep Tohoku Imp Univ Fourth Ser Biol 21:137–144

Toriumi M (1955e) Taxonomical study on freshwater Bryozoa. 13. *Hyalinella punctate* (Hancock). Sci Rep Tohoku Imp Univ Fourth Ser Biol 21:241–247

Toriumi M (1955f) Taxonomical study on freshwater Bryozoa. 14. Reconsideration on *Hyalinella toanensis* Hozawa and Toriumi. Sci Rep Tohoku Imp Univ Fourth Ser Biol 21:249–255

Toriumi M (1956a) Taxonomical study on fresh-water Bryozoa. 15. *Pectinatella gelatinosa* Oka. Sci Rep Tohoku Imp Univ Fourth Ser Biol 22:29–33

Toriumi M (1956b) Taxonomical study on fresh-water Bryozoa. 16. *Lophopodella carteri* (Hyatt). Sci Rep Tohoku Imp Univ Fourth Ser Biol 22:35–44

Toriumi M (1956c) Taxonomical study on fresh-water Bryozoa. 17. General consideration: interspecific relation of described species and phylogenic consideration. Sci Rep Tohoku Univ Fourth Ser Biol 22:57–88

Waeschenbach A, Taylor PD, Littlewood DTJ (2012) A molecular phylogeny of bryozoans. Mol Phylogenet Evol 62:718–735

Wood TS (1989) Ectoproct bryozoans of Ohio. Bull Ohio Biol Surv New Ser 8:1–70

Wood TS (2001) *Plumatella mukaii*, a new phylactolaemate bryozoan from Asia and South America. Hydrobiologia 445:51–56

Wood TS, Okamura B (2005) A new key to the freshwater bryozoans of Britain, Ireland and continental Europe, with notes on their ecology. Freshwater Biological Association, Ambleside

Yanagi N, Okada Y (1918) On a collection of Japanese Cheilostomatous Bryozoa. I. Annot Zool Jpn 9:407–429

Chapter 25
Ophiuroidea (Echinodermata): Systematics and Japanese Fauna

Masanori Okanishi

Abstract This chapter consists of two sections, providing an overview of systematics and the Japanese fauna of Ophiuroidea (brittle stars and basket stars), the most diverse class of living Echinodermata. The first section presents their body plan and the history of systematic research, with a special emphasis on the order Euryalida as an example of well-studied subtaxa. The second section describes the biodiversity of ophiuroids in Japanese waters based on a comprehensive bibliographic survey of existing literature. Currently, 342 species in 120 genera and 18 families are known from Japan, which constitutes three quarters of the number of species recorded from the North Pacific area. Of the five biogeographic zones, the temperate zone contains the highest number of species (218), with similar numbers occurring in the subtropical zone (203), including elements of the highly diverse Indo-West Pacific fauna. The number of species from middle-temperate zone (111) are also relatively high, but in other northern zones, including the cool-temperate zone (16) and subarctic zone (27), the diversity is low.

Keywords Echinodermata • Ophiuroidea • Euryalida • Systematics • Japanese fauna • Molecular phylogeny • Morphological taxonomy

25.1 Ophiuroid Systematics

25.1.1 Habitat and Shape

Ophiuroids occur on diverse benthic substrates in every ocean, distributed from polar regions to the Equator, ranging from shallow intertidal to abyssal zones as deep as 6500 m (Stöhr et al. 2012; O'Hara et al. 2014). Morphological and behavioral specializations in ophiuroids, which are mainly represented by their flexible arms, enable them to live in a wide range of habitats: under rocks or in interstices within sponges and hard corals; on muddy bottom, where some species

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can be found in aggregation (e.g., *Ophiura sarsii*; see Fujita and Ohta, 1990b); infaunally buried in sediments, with arms extended out of the bottom for filter feeding (e.g., *Amphioplus macraspis*; see Fujita and Ohta, 1990a); and on the surface of various animals such as sponges, octocorals, and hydrocorals (e.g., *Ophiothela mirabilis*; see Hendler et al., 2012).

Figure 25.1 provides an overview of morphological features used in ophiuroid systematics. Ophiuroids have a pentamerous aborally—orally flattened body with five flexible arms and a pentagonal to circular central disc (Fig. 25.1a, i). In many cases, the disc and arms can be clearly distinguished (Fig. 25.1a, i). Five jaws visible on the center of the oral side of the disc have a complex skeleton with many elements, including the oral shields, the adoral shields, and the dental plate (Fig. 25.1d, f–h). Oral papillae are articulated laterally with the jaws, whereas teeth are vertically articulated with the dental plate at the tip of each jaw (Fig. 25.1e, f). One modified oral shield that is sometimes larger than the others serves as the madreporite, which connects the water vascular system to the outside environment. Some species possess more than two madreporites (e.g., *Astroglymma sculpta* has five). The surface of the disc is usually covered by scales (Fig. 25.1c, l), which bear spines or granules in many taxa. In some species in the family Ophiomyxidae (order Ophiurida) and also in the order Euryalida, the disc is covered by thick integument, which often contains tiny, embedded dermal ossicles (Baker 1980). Genital slits are present between the basal arm segments and the oral side of the disc (Fig. 25.1c). These slits are the external opening to internal pouches called bursae.

The arm shows distinct segmentation, each segment being composed of a pair of lateral arm plates (Fig. 25.1j, m), a dorsal arm plate (Fig. 25.1k), and a ventral arm plate (Fig. 25.1b). These plates surround a central ossicle; the latter is referred to as a ‘vertebra’ in ophiuroid systematics (Fig. 25.1n, o). Arm spines are articulated with the lateral arm plates (Fig. 25.1m). The vertebrae have matching articulation on their distal and proximal sides (Fig. 25.1n, o). There are two types of vertebral articulations (steptospondylous and zygospondylous); the difference was once used as a taxonomic character for higher classification (Matsumoto 1917), but intermediate forms exist (Litvinova 1989a, b, 1996; Hotchkiss and Glass 2012). Growth bands are considered to be present on the surface of the vertebrae (Fig. 25.1p), which may be formed annually or seasonally according to some studies (Gage 1990; Wilding and Gage 1995; Dahm and Brey 1998).

In contrast to other echinoderms, ophiuroids lack a sucker-like structure on the tip of their tube feet. The animals are able to capture suspended food particles by the mucus secreted from their tube feet, which are referred to as ‘tentacles’ in ophiuroid anatomy (Emson and Woodley 1987). All tentacles emerge from tentacle pores, linearly arrayed from the oral slit to the arm tips (Fig. 25.1b, c). A pair of tentacle pores is present on every arm segment, and beside each pore, there are small plates called tentacle scales (Fig. 25.1c). Species in the order Euryalida lack tentacle scales, and instead have arm spines in the same position (Mortensen 1933; Baker 1980; McKnight 2000; Stöhr 2011; Okanishi and Fujita 2014a, b).

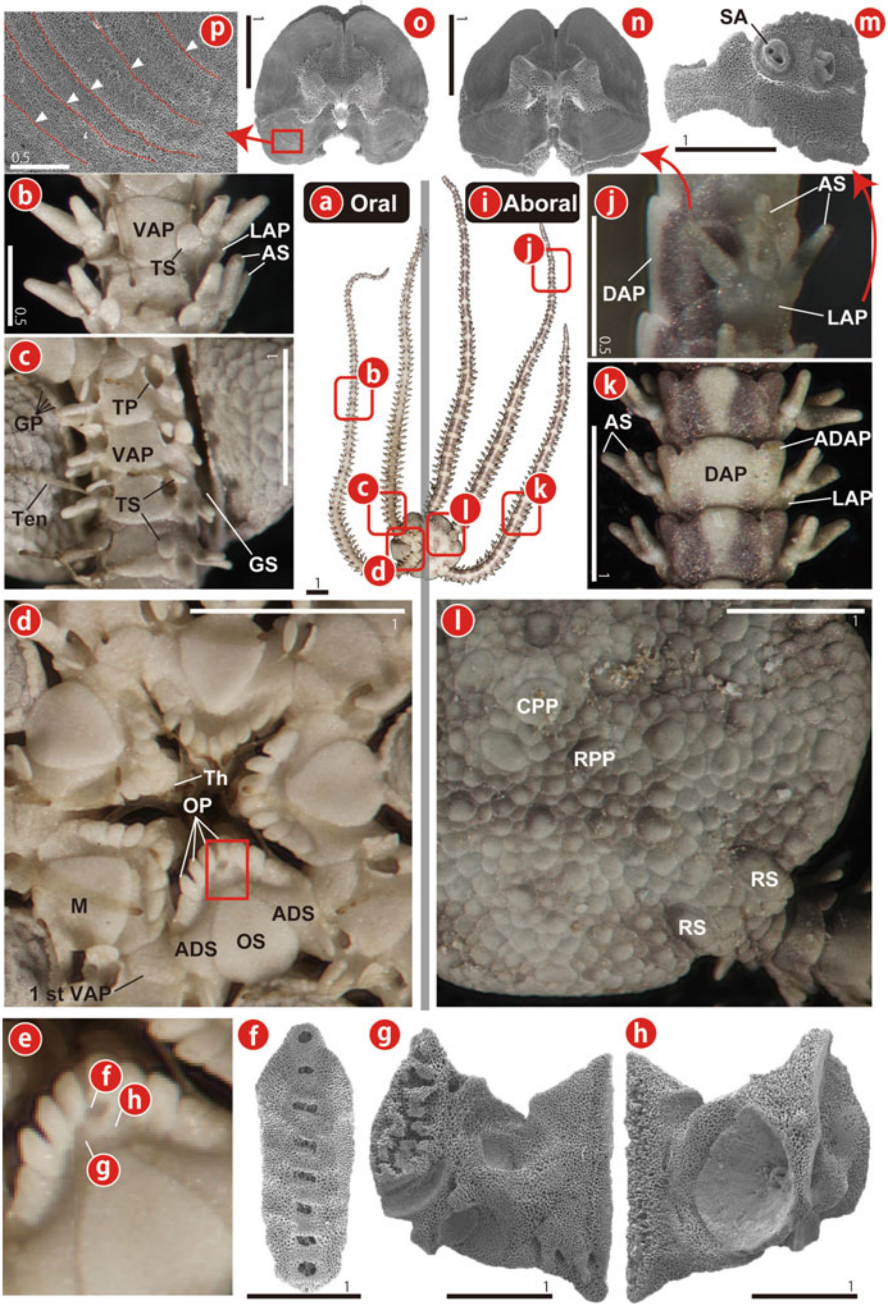

Fig. 25.1 General morphology of brittle stars shown on *Ophionereis porrecta* (**a**–**e**, **i**–**l**) and *Ophioplinthaca rudis* (**f**–**h**, **m**–**p**). **a** Oral view of the body. **b** Oral view of an arm. **c** Oral view of the disc and basal portion of an arm. **d** Oral view of the disc (the jaw skeleton indicated by an *red square* is enlarged in **e**). **e** A jaw. **f** External view of a dental plate with tooth articulations. **g** Abradial view of an oral plate (half jaw). **h** Adradial view of an oral plate. **i** Aboral view of the body. **j** Lateral view of an arm. **k** Aboral view of an arm. **l** Aboral view of the disc. **m** External

Ophiuroids are distinguished from other echinoderms by the presence of the vertebrae-shaped ambulacral ossicles, the absence of an open ambulacral groove on the oral side of the arms, the absence of an anus (found on the aboral side of the disc in sea stars), and the presence of the madreporite on the oral side of the disc in a specialized oral shield (Telford et al. 2014). However, some extinct ophiuroid taxa (e.g., family Klasmuridae) have isolated vertebrae and an open ambulacral groove (Hotchkiss et al. 1999).

25.1.2 Higher Classification

Ophiuroidea is sister to Asteroidea, together forming the taxon Asterozoa (Blake 2013; Cannon et al. 2014; O'Hara et al. 2014; Telford et al. 2014). Currently, Ophiuroidea comprises 18 families, 270 genera, and about 2100 species (Stöhr et al. 2012). The first comprehensive study of the family- and order-level relationships and classification of Ophiuroidea was done by Matsumoto (1917). Based on careful anatomic and paleontological observations covering all families of Ophiuroidea, he divided the class into two subclasses, Oegophiuroida (extinct) and Myophiuroida (containing both living and fossil members); the latter was further subdivided into four orders: Phrynophiurida, Laemophiurida, Chilophiurida, and Gnathophiurida. Each order was characterized by the presence or absence of dorsal arm plates, and also by the structures relating to genital plate articulation. Matsumoto (1917) also proposed a phylogenetic tree of the group using ontogenetic data, which include comparison of morphology in young stages and adults. However, the conclusions of Matsumoto (1917) were not universally accepted. For example, Döderlein (1927) rejected Phrynophiurida, as he recognized a distinction between Euryalae (Euryalida) and Ophiurae (Ophiurida) based on the forms of vertebral articulation (Döderlein 1927). On the other hand, Fell (1962) and Murakami (1963b) independently found that their studies of dental plates, oral plates, and gonadal morphology agreed with Matsumoto's (1917) higher classification. Subsequently, this classification was followed by a systematic review of Echinodermata from morphological perspectives for both extant and fossil taxa (Spencer and Wright 1966). Quantitative phylogenetic reconstruction of all described families (at that time) of post-Paleozoic within the class Ophiuroidea

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Fig. 25.1 (continued) view of a lateral arm plate. **n** Basal view of an isolated vertebra. **o** Distal view of an isolated vertebra (a part of the surface is indicated by a *red square*). **p** Enlarged surface of a vertebra: *arrow heads* indicate growth bands. *ADAP* accessory dorsal arm plate, *ADS* adoral shield, *AS* arm spine, *CPP* central primary plate, *DAP* dorsal arm plate, *GP* genital papillae, *GS* genital slit, *LAP* lateral arm plate, *M* madreporite, *OP* oral papillae, *OS* oral shield, *RPP* radial primary plate, *RS* radial shield, *SA* spine articulation, *Ten* tentacle, *Th* teeth, *TP* tentacle pore, *TS* tentacle scale, *VAP* ventral arm plate. *Bars* in millimeters was performed by Smith et al. (1995) based on morphological, paleontological, and molecular characters.

Reconstruction of a phylogenetic tree based on nucleotide sequences was attempted by Perseke et al. (2010), Janies et al. (2011), and Telford et al. (2014). Recently, O'Hara et al. (2014) performed a phylogenomic analysis based on 52 species covering 15 of 18 known extant families for 102,143 amino acid data (Fig. 25.2). Although the resulting molecular tree largely supported Matsumoto's (1917) classification of Gnathophiurida, Laemophiurida, and Phyrynophiurida, it clearly rejected Chilophiurida, which was shown to be polyphyletic.

Morphological information on microstructure has been rapidly accumulated by scanning electron microscopy (SEM) observations on the spine articulation and the surface ornamentation of the lateral arm plates (Baker 1980; Hendler 1988; Byrne 1994; Irimura 1991; Martynov 2010; Thuy and Stöhr 2011). Of these, the microstructure of lateral arm plates found by Thuy and Stöhr (2011) was consistent with the new molecular tree (Fig. 25.2). Needless to say, it is still important for establishing a sound higher classification system of Ophiuroidea to revisit such 'macro' structures as the mode of muscle articulation with the endoskeleton, the shape of the peristominal plates, and the type of vertebrae articulation (Matsumoto 1917).

25.1.3 Euryalida: As an Example

The order Euryalida is a small group, currently composed of 186 species (Okanishi and Fujita 2013, 2014b; Stöhr et al. 2014), which accounts for less than 10 % of the total number of species in Ophiuroidea. However, during the past few years, a number of systematic studies have been conducted on Euryalida ranging from the species to family levels, partially because this taxon is phylogenetically important for considering the evolution of the entire Ophiuroidea, within which Euryalida has long been regarded as an early stem group (Matsumoto 1915, 1917; Fell 1962; Murakami 1963b; Smith et al. 1995; Littlewood et al. 1997; Janies et al. 2011). These recent studies include descriptions of new taxa (Okanishi and Fujita 2009, 2011a; Okanishi et al. 2011c; Stöhr 2011; Parameswaran and Jallel 2012), taxonomic reviews (Okanishi and Fujita 2011b, 2014a, b; Okanishi et al. 2013, 2014), evaluation of new morphological characters (Okanishi et al. 2011c, 2013; Tajiri and Fujita 2013), and molecular phylogenetic analyses (Okanishi et al. 2011b; Okanishi and Fujita 2013).

Until recently, Euryalida had been thought to comprise four families: Asteronychidae; Asteroschematidae; Euryalidae; and Gorgonocephalidae (Smith et al. 1995). Two authors attempted to subdivide Gorgonocephalidae, based on the degree of branching of the arms (Verrill 1899) or based on internal morphological features such as presence or absence of muscles covering the basal vertebrae (Matsumoto 1915, 1917), but these revisions were not accepted by subsequent authors (Mortensen 1933; Spencer and Wright 1966; Smith et al. 1995)

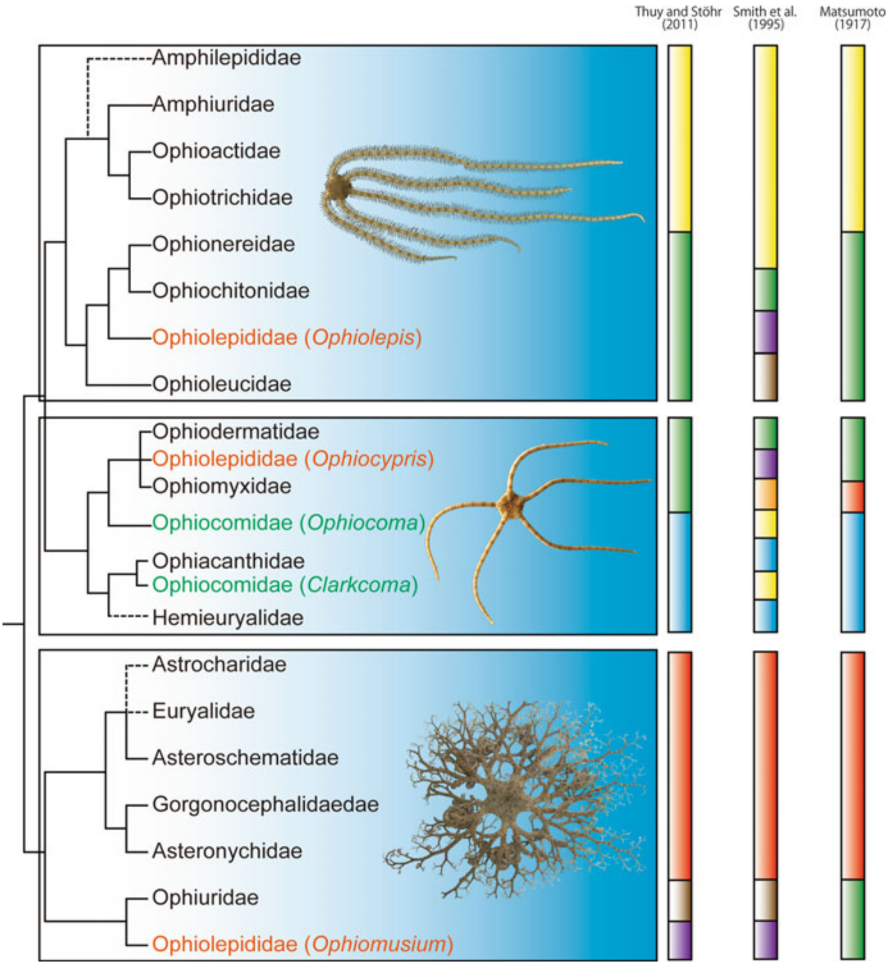

Fig. 25.2 Schematic phylogenetic tree diagram of a molecular phylogenetic tree of the families of the class Ophiuroidea based on O'Hara et al. (2014) and comparison with previous systematic studies (Matsumoto 1917; Smith et al. 1995; Thuy and Stöhr 2011). Amphilepididae, Astrocharidae, Euryalidae, and Hemieuryalidae are not used in O'Hara et al. (2014); indicated by *dashed lines*. Three higher classification schemes of Matsumoto (1917), Smith et al. (1995), and Thuy and Stöhr (2011) are shown on the *right* as follows: *yellow*, Gnathophiurida; *green*, Ophiodermatina; *purple*, Ophiolepidina; *orange*, Ophiomyxina; *blue*, Hemieuryalina; *brown*, Chilophiurida, *red*, Euryalida. Polyphyletic families are colored *green* (Ophiocomidae) and *orange* (Ophiolepididae). Generic names used in O'Hara et al. (2014) are in *brackets* (Photograph of a basket star (*Astrocladus coniferus*) was provided by Dr. Tetsuya Kato of Shirahama Aquarium, Kyoto University)

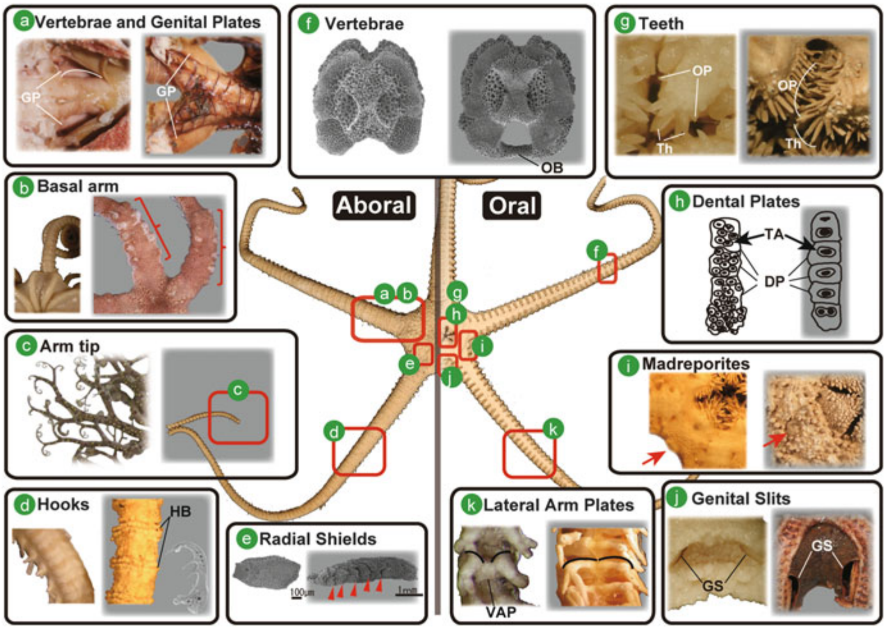

Fig. 25.3 Important characteristics that distinguish the family-level taxa of the order Euryalida. Alternative states in each character are indicated on white (*left*) and gray (*right*) backgrounds. **a** Basal vertebra and genital plates: aboral disc surface removed, translucent muscles cover the vertebrae and genital plates (*left*), muscles do not cover the vertebrae and genital plates (*right*). **b** Aboral view of the basal arms: gonads restricted to the disc (*left*), or gonads extending into the basal portion of the arms where they are enlarged (*brackets*) in width (*right*). **c** Arm tips: branching (*left*), or not branching (*right*). **d** Aboral view of the arms: hooks absent (*left*), or hook bands present (*right*; SEM image is a hook). **e** Isolated radial shields: borders of overlapped ossicles are indicated by *arrowheads*, mono-layer (*left*), or multi-layer (*right*). **f** Isolated vertebrae: oral groove is open (*left*), or is closed by an oral bridge (*right*). **g** Jaws: a few rudimentary oral papillae on the lateral side of each jaw (*left*), or spiniform oral papillae on the lateral side of each jaw (*right*). **h** Sketches of isolated dental plates, modified from Murakami (1963b): the number of tooth articulations on each section of the dental plate are several (*left*), or one, rarely two (*right*). **i** Oral views of discs, a madreporite (indicated by an *arrow*) is on edge of disc (*left*), or is halfway between oral frame and edge of disc (*right*). **j** Lateral side of discs: two long genital slits extending from base of arm to aboral edge of disc (*left*), or pore-like genital slits on lateral side of disc distant from base of arm and located near aboral edge of disc (*right*). **k** Oral view of arms; each lateral arm plate is indicated by an arc: a pair of lateral arm plates are separated by ventral arm plates (*left*), or the lateral arm plates are in contact (*right*). *DP* dental plate, *GS* genital slit, *GP* genital plate, *HB* hook bands, *OB* oral bridge, *OP* oral papillae, *TA* tooth articulation, *Th* teeth, *VAP* ventral arm plate

(Figs. 25.3, 25.4). As a result of molecular studies based on the mitochondrial 16S rRNA and COI and nuclear 18S rRNA genes, Okanishi et al. (2011b) and Okanishi and Fujita (2013) revised the traditional taxonomy so that morphological characters are congruent with the newly defined family-level taxa as follows: the superfamily Euryaloidea contains three families: Asteroschematidae, Euryalidae, and

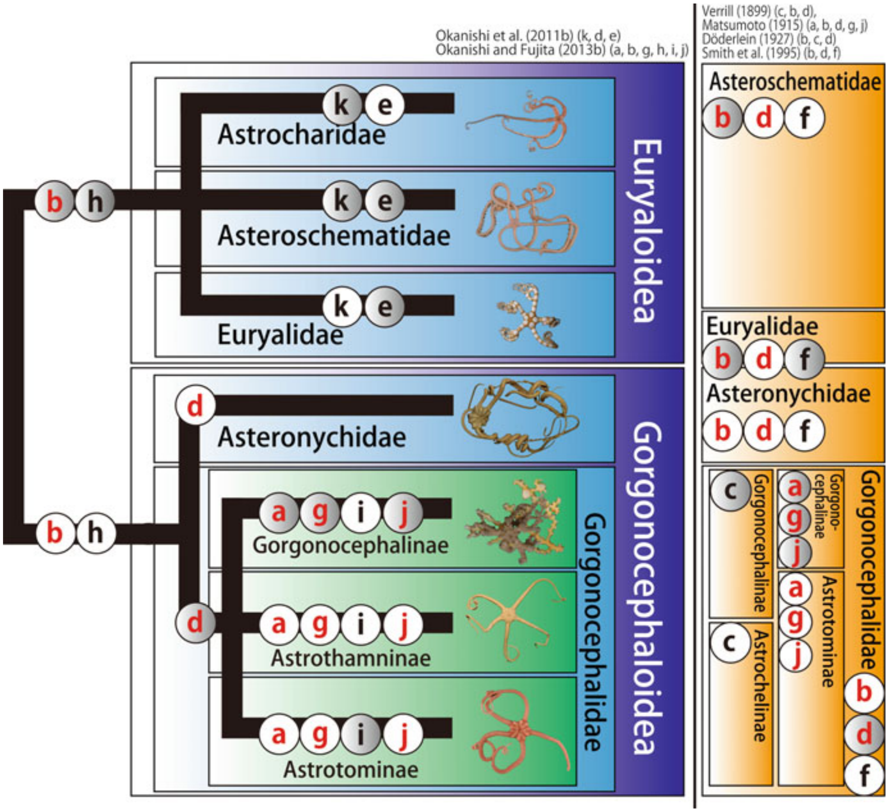

Fig. 25.4 Schematic diagram of euryalid evolutionary tree (Okanishi et al. 2011b; Okanishi and Fujita 2013). Previous classifications based on morphological characters (Verrill 1899; Matsumoto 1917; Smith et al. 1995) are shown on the *right*. Letters in *circle* (**a**–**k**) and *colors* (*white or gray*) correspond to the characters and their states, respectively, shown in Fig. 25.3. *Red letters* in *circle* denote the characters that are used both in the traditional and new classification systems; the former was based on morphology and the latter is based on molecular phylogeny. Character states used in each author are shown after each author name. In molecular phylogeny, superfamilies, families, and subfamilies are assigned to *dark blue*, *blue*, and *green boxes*, respectively

Astrocharidae; and the superfamily Gorgonocephaloidea contains two families: Asteronychidae and Gorgonocephalidae; the latter contains three subfamilies: Astrotominae, Astrothamninae, and Gorgonocephalinae (Figs. 25.3 and 25.4).

25.2 Japanese Ophiuroids

The first comprehensive surveys of the Japanese ophiuroid fauna were undertaken by the HMS *Challenger* (1873–1876) and the USFC Steamer *Albatross* (1883–1921) (Lyman 1879, 1882; Clark 1911). The first faunistic study focusing specifically on the Japanese coast was undertaken by Matsumoto (1915, 1917). He summarized all known distributions of Japanese ophiuroids and described 27 new species. He concluded that 232 valid species were distributed along the Japanese coast (Matsumoto 1915, 1917). Since his ground-breaking studies, Japanese waters have been shown to possess a diverse ophiuroid fauna (Matsumoto 1918, 1941; Döderlein 1927, 1930; Mortensen 1933; Murakami 1942, 1943b, c, 1944a, b, 1963a; Djakonov 1954; Irimura 1968a, b, 1969, 1979, 1981, 1982, 1990, 1991; Saba et al. 1982; Rho and Shin 1983, 1987; Fujita and Ohta 1990a, b; Nomura 1993; Fujita 1996, 1998; Shin and Rho 1996; Fujita et al. 1997, 2004, 2006, 2009, 2011, 2014; Irimura and Kubodera 1998; Irimura and Yoshino 1999; Fujita and Saba 2000; Fujita and Hendler 2001; Irimura et al. 2001; Ishida et al. 2001; Irimura and Tachikawa 2002; Fujita and Kohtsuka 2003; Fujita and Irimura 2005; Komatsu et al. 2007; Okanishi and Fujita 2009, 2011a, b, 2014a; Okanishi et al. 2011a, 2014). At present, 18 families, 120 genera, and 342 valid species have been reported around Japan. According to a review of the geographic distribution of Ophiuroidea by Stöhr et al. (2012), the number of species in the waters around Japan is comparable with that of the West Atlantic (333) and South Pacific (350), exceeding those of the Arctic (73), North Atlantic (237), East Pacific (183), East Atlantic (117), South America (120), South Africa (199), and Antarctic (123). Only the vast Indo-Pacific region (831) is significantly more diverse. The high diversity of ophiuroid species in Japan seems contradictory with the relatively narrow coastline on a world scale (30,000 km long). Many factors such as habitats, continental plates, ocean currents, and geographic zones must affect the composition of Japanese fauna. Among them, this number is no doubt related to the wealth of habitats on the Japanese coast. This includes diverse temperature regimes ranging from the subarctic to the subtropical temperate zones, a wide depth range between 0 and 9780 m in the Izu–Ogasawara Trench, and a huge variety of topography—bays, beaches, island seas, muddy ground, rocky shores, coral reefs, sea mounts, and trenches (Fujikura et al. 2010).

Japan can be divided into five regions: subarctic zone (SA), cool-temperate zone (CT), middle-temperate zone (MT), temperate zone (TM), and a subtropical zone (ST) (Nishimura 1981). A breakdown of ophiuroid taxonomic diversity in each region is shown in Fig. 25.5 and Appendix 1. The biodiversity of ophiuroids is likely to be higher in the southern part of Japan (Okanishi, personal observation). This possible correlation of diversity with latitude was also observed by Stöhr et al. (2012), who showed that species number in the Pacific Area is smaller in high-latitude regions than low-latitude ones. In Japan, richness of diversity in the south part may be the result of the ingression of Indo-Pacific species, which are brought by the warm Kuroshio Current from Southwestern Asia (Nishimura 1981; Stöhr et al. 2012). A boundary between the Kuroshio Current and the cold Oyashio Current from Okhotsk Sea exists in the MT region. Therefore, influence of the Kuroshio Current diminishes in this region and the species diversity is lower than in the southern part. Species diversity in CT and SA is much lower because the influence of the Kuroshio Current is very minor. In the south part of Japan, the species number in the southernmost region (ST, 203 species) is below that of the

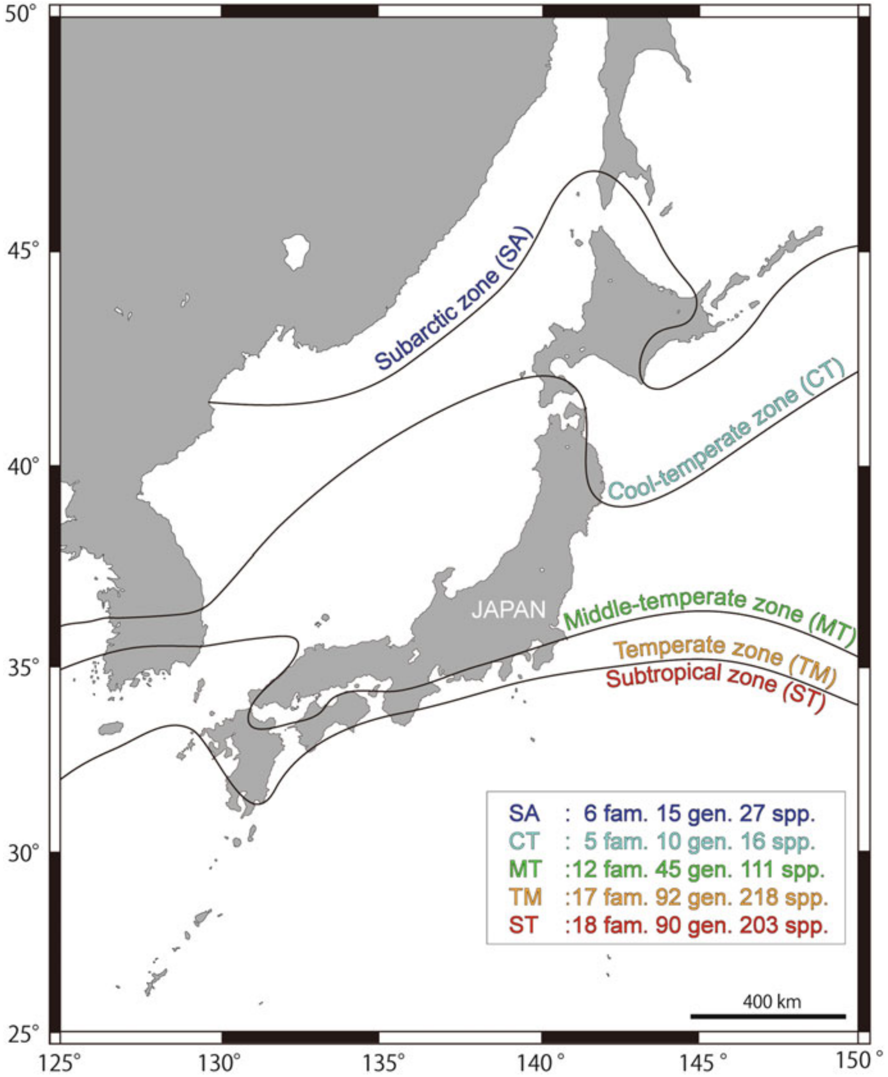

Fig. 25.5 Marine biogeographic regions in Japan. (Modified from Nishimura 1981). The number of families, genera, and species in each region are shown in a *box*

next northern region (TM, 218 species), which may be related to the richness of habitats, such as bays and channels, in the northern region in contrast to the ST (Fig. 25.5). Furthermore, surveys in the northern area include a wider depth range, whereas surveys of the subtropical zone have been restricted mostly to deep waters (e.g., Irimura and Kubodera 1998; Fujita and Irimura 2005; Okanishi et al. 2011a), with a paucity of data from shallow waters (e.g., Irimura and Tachikawa 2002).

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Appendix 1

Species list of Japanese Ophiuroidea. Classifications followed Smith et al. (1995) and Stöhr et al. (2014). Numbers in column of climate regions indicate references as follows: (1) Baranova (1964), (2) Djakonov (1954), (3) Döderlein (1902), (4) Döderlein (1911), (5) Döderlein (1927), (6) Döderlein (1930), (7) Fujita (1996), (8) Fujita et al. (1997), (9) Fujita (1998), (10) Fujita and Saba (2000), (11) Fujita and Hendler (2001), (12) Fujita (2003), (13) Fujita and Kohtsuka (2003), (14) Fujita et al. (2004), (15) Fujita and Irimurra (2005), (16) Fujita et al. (2006), (17) Fujita et al. (2009), (18) Fujita et al. (2014), (19) Clark (1908), (20) Clark (1911), (21) Clark (1915), (22) Irimura (1968b), (23) Irimura (1969), (24) Irimura (1979), (25) Irimura (1981), (26) Irimura (1982), (27) Irimura (1990), (28) Irimura (1991), (29) Irimura and Kubodera (1998), (30) Irimura and Yoshino (1999), (31) Irimura et al. (2001), (32) Irimura and Tachikawa (2002), (33) Ishida et al. (2001), (34) Jangoux et al. (1987), (35) Koehler (1907), (36) Komatsu et al. (2007), (37) Lyman (1879), (38) Lyman (1882), (39) Matsumoto (1911), (40) Matsumoto (1912a), (41) Matsumoto (1912b), (42) Matsumoto (1912c), (43) Matsumoto (1912d), (44) Matsumoto (1915), (45) Matsumoto (1917), (46) Matsumoto (1918), (47) Matsumoto (1941), (48) McKnight (2000), (49) Mortensen (1911), (50) Mortensen (1927), (51) Mortensen (1933), (52) Murakami (1942), (53) Murakami (1943a), (54) Murakami (1943c), (55) Murakami (1943b), (56) Murakami (1944b), (57) Murakami (1963a), (58) Nomura (1993), (59) Okanishi and Fujita (2009), (60) Okanishi et al. (2011d), (61) Okanishi and Fujita (2011a), (62) Okanishi and Fujita (2011b), (63) Okanishi et al. (2011c), (64) Okanishi and Fujita (2014a), (65) Rho and Kim (1966), (66) Rho and Shin 1987, (67) Rho and Shin (1983), (68) Rowe and Gates (1995), (69) Saba et al. (1982), (70) Shin and Rho (1996), (71) Verrill (1869).

Order	Family	Species					Subtropical	Temperate	Middle temperate	Cool temperate	Subarctic	?
Euryalida	Asteronychidae	*Asteronyx*		*loveni*		Müller & Troshel 1842	63	39	28	43, 45		2, 50
		Asteronyx		*niger*		Djakonov 1954					2	
		Astrodia		*abyssicola*		Lyman 1879			64			
	Asteroschematidae	*Asteroschema*		*ferox*		Koehler 1904	15					
		Asteroschema		*glaucum*		Matsumoto 1911		21, 39, 44				
		Asteroschema		*hemigymnum*		Matsumoto 1911		21, 39, 45				
		Asteroschema		*tubiferum*		Matsumoto 1911	29	39				
		Asteroschema		*yaeyamensis*		Murakami 1944	55					
		Astrocharis		*ijimai*		Matsumoto 1911	28	39, 44, 45				
		Astrocharis		*monospinosa*		Matsumoto 1911	62					
		Ophiocreas		*abyssicola*		Lyman 1879		38				37
		Ophiocreas		*caudatus*		Lyman 1879		4, 27, 34, 37, 38, 39, 45				
		Ophiocreas		*glutinosum*		Döderlein 1911		4, 34, 41, 45				
		Ophiocreas		*japonicus*		Koehler 1907		4, 19, 21, 34, 35, 39, 45, 48				
		Squamophis		*amamiensis*		Okanishi & Fujita 2009		59				
	Euryalidae	*Astroceras*		*annulatum*		Mortensen 1933a	25, 32, 51, 63, 69	5, 23, 26, 45, 51, 56, 66, 70				
		Astroceras		*calix*		Murakami 1944	55					
		Astroceras		*compar*		Koehler 1904	51, 63					
		Astroceras		*coniunctum*		Murakami 1944	55					
		Astroceras		*paucispinum*		Murakami 1944	55					
		Astroceras		*pergamenum*		Lyman 1879	25	5, 21, 23, 26, 37, 39, 42, 45				20
		Euryale		*aspera*		Lamarck 1816	45					38
		Sthenocephalus		*anoplus*		(H.L. Clark 1911)	21, 29, 45, 51					
		Trichaster		*acanthifer*		Döderlein 1927	?					4
		Trichaster		*flagellifer*		von Martens 1866	22, 25, 45	23, 56				
		Trichaster		*palmiferus*		(Lamarck 1816)	20					

	Gorgonocephalidae	*Asteroporpa*	(*Asteroporpa*)	*hadracantha*		H.L. Clark 1911	25, 32, 55, 63	4, 6, 20, 21, 26, 28, 41, 45, 51				
		Asteroporpa	(*Astromoana*)	*koyoae*		Okanishi & Fujita 2011a	61					
		Asteroporpa	(*Astromoana*)	*muricatopatella*		Okanishi & Fujita 2011a	61					
		Astroboa		*arctos*		Matsumoto 1915	22, 69	23, 26, 28, 44, 45, 56	33			
		Astroboa		*globifera*		(Döderlein 1902)	29	3, 4, 45				
		Astroboa		*nuda*		(Lyman 1874)		4				4
		Astrochele		*laevis*		H.L. Clark 1911			18		2	
		Astrochele		*pacifica*		Okanishi et al. 2011		60				
		Astrocladus		*annulatus*		(Matsumoto 1912)	22, 25, 29	23, 41	33			
		Astrocladus		*coniferus*		(Döderlein 1902)	3, 4, 22, 35, 34, 55	3, 20, 21, 23, 26, 27, 34, 41, 45, 56, 65, 69	13, 14, 24, 33,			
		Astrocladus		*exiguus*		(Lamarck 1816)	20, 25					68
		Astrocladus		*ludwigi*		(Doderlein 1896)		66				
		Astroclon		*propugnatoris*		Lyman 1879	29, 51, 56					
		Astroclon		*suensoni*		Mortensen 1911	6	49				
		Astrocrius		*murrayi*		(Lyman 1879)		4				
		Astrocrius		*sobrinus*		(Matsumoto 1912)		4, 6, 40, 44, 45				
		Astrodendrum		*sagaminum*		(Döderlein 1902)	20, 29, 55	3, 4, 5, 26, 28, 34, 45	33			
		Astroglymma		*sculptum*		(Döderlein 1896)	25, 55, 63					
		Astrohelix		*bellator*	*paucidens*	(Mortensen 1933a)	51					
		Astrohelix		*bellator*	*bellator*	(Koehler 1904)	55					
		Astrothamnus		*echinaceus*		(Matsumoto 1912)	51	41, 44				
		Astrothorax		*misakiensis*		Döderlein 1911		4, 6, 34				
		Astrothrombus		*chrysanthi*	*ornatus*	Mortensen 1933	51		18			
		Astrothrombus		*chrysanthi*	*chrysanthi*	Matsumoto 1918			46			
		Gorgonocephalus		*dolichodactylus*		Döderlein 1911	28	4, 33, 34, 45				
		Gorgonocephalus		*eucnemis*		(Müller & Troschel 1842)		3, 4, 27, 34, 45	24, 33		5	1, 2, 71
		Gorgonocephalus		*tuberosus*		Döderlein 1902		3, 4, 27, 33, 34, 67	13			

(continued)

Order	Family	Species					Subtropical	Temperate	Middle temperate	Cool temperate	Subarctic	?
Ophiurida	Amphilepididae	*Amphilepis*		*pycnostoma*		H.L. Clark 1911	45	8				
		Amphilepis		*tenuis*		Lyman 1879	45					
		Histampica		*umbonata*		(Matsumoto 1915)		45				
	Amphiuridae	*Amphiodia*		*crateodoneta*		H.L. Clark 1911			13, 28		45	
		Amphiodia		*fissa*		H.L. Clark 1911				33		
		Amphioplus	(*Amphichilus*)	*trichoides*		Matsumoto 1917		23, 45, 69	32, 54			
		Amphioplus	(*Amphioplus*)	*ancistrotus*		H.L. Clark 1911		8, 26, 28, 31, 45	45			
		Amphioplus	(*Amphioplus*)	*macraspis*		(H.L. Clark 1911)		28, 45	7		45	
		Amphioplus	(*Amphioplus*)	*psilochora*		(H.L. Clark 1911)		45				
		Amphioplus	(*Amphioplus*)	*rhadinobrachius*		H.L. Clark 1911		8, 26, 28, 45	18			
		Amphioplus	(*Lymanella*)	*depressus*		(Ljungman 1867)	32					
		Amphioplus	(*Lymanella*)	*japonicus*		(Matsumoto 1915)	15, 25, 45	23, 26, 31, 69	45, 47			
		Amphioplus	(*Lymanella*)	*laevis*		(Lyman 1874)	25	45, 69	14, 54			
		Amphioplus	(*Unioplus*)	*cernunus*		(Lyman 1879)		45				
		Amphioplus	(*Unioplus*)	*glauca*		(Lyman1879)		8, 28, 45				
		Amphioplus		*asterictus*		H.L. Clark 1915		69	13			
		Amphioplus		*diactitus*		Murakami 1943		54, 69				
		Amphioplus		*euryaspis*		(H.L. Clark 1911)		45	33		45	
		Amphioplus		*hexacanthus*		H.L. Clark 1911	45					
		Amphipholis		*kochii*		Lütken 1872		23, 45, 69	13, 24, 47	36, 45		
		Amphipholis		*microdiscoida*		H.L. Clark 1915		18				
		Amphipholis		*microdiscus*		(Lütken 1856)		45	13			
		Amphipholis		*pugetana*		Lyman 1860			45, 47	45	45	
		Amphipholis		*sobrina*		Matsumoto 1917	9	45	18			
		Amphipholis		*tetracantha*		Matsumoto 1941			33, 47			
		Amphipholis		*squamata*		(Delle Chiaje 1828)	15, 25, 32, 45	23, 26, 31, 45, 69	10, 24			
		Amphistigma		*minuta*		H.L. Clark 1938	9					
		Amphiura	(*Amphiura*)	*acrystata*		H.L. Clark 1911		8, 26				
		Amphiura	(*Amphiura*)	*diastata*		(Murakami 1942)		52				
		Amphiura	(*Amphiura*)	*digitula*		(H.L. Clark 1911)		31, 45	45			
		Amphiura	(*Amphiura*)	*duncani*		Lyman 1882		23	14			45
		Amphiura	(*Amphiura*)	*euopla*		H.L. Clark 1911		23, 26, 28, 31, 45, 69	18			

		Amphiura	(*Amphiura*)	*grandisquama*		Lyman 1869	15	8, 47				
		Amphiura	(*Amphiura*)	*leptotata*		H.L. Clark 1915	32					
		Amphiura	(*Amphiura*)	*macraspis*		H.L. Clark 1911		8				
		Amphiura	(*Amphiura*)	*micraspis*		H.L. Clark 1911		8, 23, 45	14			
		Amphiura	(*Amphiura*)	*trachydisca*		H.L. Clark 1911	15	8, 26, 28, 45,				
		Amphiura	(*Fellaria*)	*ecnomiotata*		H.L. Clark 1911	8, 25					
		Amphiura	(*Fellaria*)	*octacantha*		H.L. Clark 1915	58	52				
		Amphiura	(*Fellaria*)	*vadicola*		Matsumoto 1915	25, 45		13			
		Amphiura	(*Ophiopeltis*)	*aestuarii*		Matsumoto 1915		23, 45, 69	54			
		Amphiura		*acacia*		Lyman 1879		45				
		Amphiura		*acrystata*		H.L. Clark 1911	45	45	45			
		Amphiura		*bellis*		Lyman 1879	45	8, 45				
		Amphiura		*carchara*		H.L. Clark 1911		8, 45				
		Amphiura		*iridoides*		Matsumoto 1917	15	23, 45, 69	18			
		Amphiura		*kandai*		Murakami 1942		31	14			
		Amphiura		*koreae*		Duncan 1879	45	8, 28, 45	7, 13, 28, 45			
		Amphiura		*leptobrachia*		H.L. Clark 1915		52	33			
		Amphiura		*pachybactra*		Murakami 1942		52				
		Amphiura		*psilopora*		H.L. Clark 1911			18			
		Amphiura		*sinicola*		Matsumoto 1915		69	33, 47			
		Amphiura		*syntaracha*		H.L. Clark 1915		23	24			
		Dougaloplus		*acanthinus*		(H.L. Clark 1911)		8, 28, 45				
		Dougaloplus		*dividua*		(Matsumoto 1917)		45				
		Ophiocentrus		*koehleri*		Gislen 1926	32	31	14			
		Ophiocentrus		*tokiokai*		Irimurra 1981	25					
		Ophiocentrus		*verticillatus*		(Döderlein 1896)		23, 69				
		Ophiodaphne		*formata*		(Koehler 1905)	25	31				
	Hemieuryalidae	*Ophiomoeris*		*nodosa*		(Koehler 1905)	55					
		Ophiomoeris		*obstricta*		(Lyman 1878)	28, 45					

(continued)

Order	Family	Species					Subtropical	Temperate	Middle temperate	Cool temperate	Subarctic	?
	Ophiacanthidae	*Ophiacantha*		*acanthinotata*		H.L. Clark 1911	45	16, 45	33			
		Ophiacantha		*adiaphora*		H.L. Clark 1911		45	7		45	
		Ophiacantha		*aenigmatica*		Matsumoto 1917		45				
		Ophiacantha		*bathybia*		H.L. Clark 1911	28					
		Ophiacantha		*bidentata*		(Bruzelius 1905)			45		45	
		Ophiacantha		*dallasii*		Duncan 1879						45
		Ophiacantha		*duplex*		Koehler 1897	45	69	33			
		Ophiacantha		*levispina*		Lyman 1878	8, 15, 25, 28, 29, 45	26, 31, 45, 69	33			
		Ophiacantha		*lophobrachia*		H.L. Clark 1911	45					
		Ophiacantha		*omoplata*		H.L. Clark 1911		13, 28				45
		Ophiacantha		*pentagona*		Koehler 1897	45	16, 31, 45	33			
		Ophiacantha		*rhachophora*		H.L. Clark 1911	8, 15, 45		45			
		Ophiacantha		*rhachophora*		H.L. Clark 1911		16, 28, 45				
		Ophiacantha		*rosea*		Lyman 1878		29, 45				
		Ophiacantha		*trachybactra*		H.L. Clark 1911			7	28		
		Ophiacantha		*vorax*		H.L. Clark 1911		16				
		Ophiacanthella		*acontophora*		H.L. Clark 1911				45		
		Ophiambix		*aculeatus*		Lyman 1880	45					
		Ophientrema		*euphylacteum*		(H.L. Clark 1911)		45				
		Ophientrema		*scolopendricum*		(Lyman 1883)		45				
		Ophientrema		*valenciennesi*		(Lyman 1879)	55					
		Ophiocamax		*vitrea*		Lyman 1878	15, 29, 45	16				
		Ophiolebes		*asaphes*		H.L. Clark 1911			45	45	45	
		Ophiolebes		*brachygnatha*		H.L. Clark 1911					45	
		Ophiolebes		*sagaiensis*		Irimura 1982		26				
		Ophiolebes		*tuberosus*		Matsumoto 1915		45	7			
		Ophiolimna		*bairdi*		(Lyman 1883)	8, 28, 45		7			
		Ophiolimna		*diastata*		(H.L. Clark 1911)	45	16, 31				
		Ophiolimna		*perfida*		(H.L. Clark 1911)		45				
		Ophiologimus		*hexactis*		H.L. Clark 1911		8, 16, 45				
		Ophiomitra		*leucorhabdotus*		(H.L. Clark 1911)	45	16				
		Ophiomitrella		*ikedai*		Murakami 1944	55	16				
		Ophiomitrella		*polyacantha*		(H.L. Clark 1911)	45	16				

		Ophiomitrella		*stellifera*		Matsumoto 1917		16, 26, 45				
		Ophiophrura		*liodisca*		H.L. Clark 1911		45				
		Ophiophthalmus		*cataleimmoidus*		(H.L. Clark 1911)		16, 27, 45			45	
		Ophiophthalmus		*hylacantha*		(H.L.Clark 1911)		8, 45				
		Ophiophthalmus		*normani*		(Lyman 1879)	8, 45	16, 27, 45	7	45	45	
		Ophioplinthaca		*bythiaspis*		(H.L. Clark 1911)	15	45				
		Ophioplinthaca		*codonomorpha*		(H.L. Clark 1911)		45				
		Ophioplinthaca		*lithosora*		(H.L. Clark 1911)	45					
		Ophioplinthaca		*pulchra*		Koehler 1904		16				
		Ophioplinthaca		*rudis*		(Koehler 1897)	45	27, 45				
		Ophiopristis		*luctuosa*		Koehler 1904		16, 69				
		Ophiosemnotes		*tylota*		(H.L. Clark 1911)			45			
		Ophiothamnus		*hadbrotatus*		(H.L. Clark 1911)	45					
		Ophiothamnus		*venustus*		Matsumoto 1915		16, 26, 45				
		Ophiotholia		*spathifer*		(Lyman 1879)		8, 16, 26, 31, 45				
		Ophiotoma		*megatrema*		(H.L. Clark 1911)						45 (ST?)
		Ophiotreta		*gratiosa*		(Koehler 1897)		16, 28				
		Ophiotreta		*inutilis*		Koehler 1904		69				
		Ophiotreta		*stimulea*		(Lyman 1878)	45	45				
		Ophiotreta		*valenciennesi*		(Lyman 1879)		16, 45				
		Ophiuroconis		*monolepis*		Matsumoto 1915		16				
		Ophiurothamnus		*dicycla*		H.L. Clark 1911	45	45				
	Ophiactidae	*Histampica*		*umbonata*		(Matsumoto 1915)		8				
		Ophiactis		*affinis*		Duncan 1879	25	69	10, 13			45
		Ophiactis		*brachygenys*		H.L. Clark 1911	15, 45	8, 27, 45	33			
		Ophiactis		*dyscrita*		H.L. Clark 1911	32	23, 45	33			
		Ophiactis		*hemiteles*		H.L. Clark 1915	32					
		Ophiactis		*profundi*		Lütken & Mortensen 1899	8, 15	45	45			
		Ophiactis		*gymnochora*		H.L. Clark 1911	45					
		Ophiactis		*macrolepidota*		Marktanner-Truneretscher 1887	15, 25	23, 45	45			
		Ophiactis		*modesta*		Brock 1888	25, 32	23	33			
		Ophiactis		*plana*		Lütken 1856		69	13			

(continued)

Order	Family	Species					Subtropical	Temperate	Middle temperate	Cool temperate	Subarctic	?
		Ophiactis		*profundi*		Müller & Troschel 1842	25	31	33			
		Ophiactis		*savignyi*		Müller & Troschel 1842	25, 32	23, 26, 31, 45, 69	13, 24			
		Ophiopholis		*aculeata*		Linnaeus 1767		52	24, 45	36	45	
		Ophiopholis		*brachyactis*		H.L. Clark 1911	15, 25, 27	8, 26, 31, 45	13			
		Ophiopholis		*japonica*		Lyman 1879	9	8, 27	7, 13	36		
		Ophiopholis		*mirabilis*		Duncan 1879		26, 27, 31, 45, 69	13, 45, 47		45	
	Ophiochitonidae	*Ophiochiton*		*fastigatus*		Lyman 1878	32, 45	8, 26, 27, 45, 69				
		Ophioplax		*lamellosa*		Matsumoto 1915	55	45				
	Ophiocomidae	*Ophiarthrum*		*elegans*		Peters 1851	45					
		Ophiarthrum		*picta*		(Müller & Troschel 1842)	53					
		Ophiocoma	(*Breviturma*)	*brevipes*		Peters 1851	45	57				
		Ophiocoma	(*Breviturma*)	*dentata*		(Müller & Troschel 1842)	25, 32	69				
		Ophiocoma	(*Breviturma*)	*doederleini*		de Loriol 1899	32					
		Ophiocoma		*erinaceus*		(Müller & Troschel 1842)	32					
		Ophiocoma		*pica*		(Müller & Troschel 1842)	32					
		Ophiocoma		*pusilla*		(Brock 1888)	32					
		Ophiocoma		*scolopendrina*		(Lamarck 1816)	32, 45					
		Ophiocomella		*sexradia*		(Duncan 1887)	32					
		Ophiomastix		*annulosa*		(Lamarck 1816)	32, 45					
		Ophiomastix		*asperula*		Lütken 1869	53					
		Ophiomastix		*caryophyllata*		Lütken 1869	53					
		Ophiomastix		*janualis*		Lyman 1871	45					
		Ophiomastix		*mixta*		Lütken 1869	25, 32	26, 33, 45, 69				
		Ophiopsila		*pantherina*		Koehelr 1898		31				
		Ophiopsila		*squamifera*		Murakami 1963		23, 26, 69				
	Ophiodermatidae	*Bathypectinura*		*heros*		Lyman 1879		27, 39				
		Cryptopelta		*longibrachialis*		Koehler 1931	32					
		Ophiarachna		*incrassata*		(Lamarck 1816)	25, 32, 45	69				

		Ophiarachna		*oshimai*		Murakami 1943	32					
		Ophiarachna		*robillardi*		de Loriol 1893	32					
		Ophiarachnella		*gorgonia*		(Müller & Troschel 1842)	25, 32, 45	26, 45, 69	13, 24			
		Ophiarachnella		*infernalis*		(Müller & Troschel 1842)	32, 33, 45	45				
		Ophiarachnella		*megalaspis*		H.L. Clark 1911	15, 45	45				
		Ophiarachnella		*septemspinosa*		(Müller & Troschel 1842)	53					
		Ophiarachnella		*sphenischi*		(Müller & Troschel 1842)	32					
		Ophiarachnera		*differens*		(Murakami 1944)	25	23				
		Ophioconis		*cincta*		Brock 1888	32					
		Ophioconis		*cupida*		(Koehler 1905)		31				
		Ophiodiscrita		*pacifica*		(Murakami 1943)	9					
		Ophiodyscrita		*instratus*		Murakami 1944		56				
		Ophiopeza		*spinosa*		(Ljungman 1867)	53					
		Ophiopsammus		*aequalis*		(Lyman 1880)	15, 27					
		Ophiopsammus		*anchista*		(H.L. Clark 1911)	25, 32, 45	26, 45, 69	13, 24			
		Ophiopsammus		*assimilis*		(Bell 1888)			33			
		Ophiostegustes		*novaecaledoniae*		Guille & Vadon 1985	9					
		Ophiuroconis		*monolepis*		Matsumoto 1915		8, 45	14			
		Ophiurodon		*grandisquama*		Koehler 1904		8, 23, 45				
	Ophiolepididae	*Aspidophiura*		*forbesi*		(Duncan 1879)	25	8	45			
		Aspidophiura		*watasei*		Matsumoto 1915		45				
		Ophiolepis		*cincta*		Müller & Troschel 1842	58					45
		Ophiolepis		*superba*		H.L. Clark 1915	32					
		Ophiomusium		*granosum*		Lyman 1878		45				
		Ophiomusium		*laqueatum*		Lyman 1878	45					
		Ophiomusium		*luetokeni*		Lyman 1878	45					
		Ophiomusium		*lunare*		Lyman 1878	15, 45					

(continued)

Order	Family	Species					Subtropical	Temperate	Middle temperate	Cool temperate	Subarctic	?
		Ophiomusium		*lymani*		Thomson 1873	45	27, 45				
		Ophiomusium		*scalare*		Lyman 1878	25	27, 45	33			
		Ophiomusium		*simplex*		Lyman 1878	15, 25, 45					
		Ophiomusium		*trychnum*		H.L. Clark 1911	25	8, 26, 27, 45, 69				
		Ophiopenia		*disacantha*		H.L. Clark 1911			45			
		Ophiopenia		*tetracantha*		H.L. Clark 1911			18			
		Ophioplocus		*giganteus*		Irimura 1999	30					
		Ophioplocus		*imbricatus*		(Müller & Troschel 1842)	32, 45					
		Ophioplocus		*japonicus*		H.L. Clark 1911	25	26, 45, 69	10, 13, 24			
		Ophiosphalma		*cancellatum*		H.L. Clark 1914		8, 28, 45, 69				
		Ophiosphalma		*jolliense*		McClendon 1980		8, 45, 69				
		Ophioteichos		*utinomii*		(Irimura 1968)	25	22				
		Ophiozonella		*bispinosa*		Koehler 1897	45					
		Ophiozonella		*longispina*		(H.L. Clark 1908)	25	8, 26, 27, 45, 69	7			
		Ophiozonella		*oedilepis*		(Murrakami 1942)	25	31				
		Ophiozonella		*platydisca*		(H.L. Clark 1911)		27, 45				
		Ophiozonella		*polyplax*		(H.L. Clark 1911)	45	27				
		Ophiozonella		*projecta*		(Koehler 1905)	25, 32, 45	8, 26, 45, 69				
		Ophiozonoida		*leucus*		(Murakami 1943)	32					
	Ophioleucidae	*Ophiernus*		*adspersus*		Lyman 1883	45	27				
		Ophioleuce		*brevispinum*		(H.L. Clark 1911)	45					
		Ophioleuce		*seminudum*		Koehler 1904	15, 45	8, 26, 31, 45	18			
		Ophiopallas		*brevispina*		(Lyman 1878)	32					
		Ophiopallas		*paradoxa*		Koehler 1904	15					
		Ophiotrochus		*longispinus*		H.L. Clark 1911		45				
	Ophiomyxidae	*Astrogymnotes*		*irimurai*		Baker et al. 2001	32					
		Ophiobrachion		*hamispinum*		Murakami 1944	55					
		Ophiobyrsa		*acanthinobrachia*		H.L. Clark 1911	15					

		Ophiobyrsa		*strictima*		Murakami 1944	55					
		Ophiodera		*bengalensis*		(Koehler 1897)	15	27				
		Ophiohyalus		*gotoi*		Matsumoto 1915		45				
		Ophiohymen		*gymnodiscus*		H.L. Clark 1911	45					
		Ophioleptoplax		*megapora*		H.L. Clark 1911	45					
		Ophiomyxa		*anisacantha*		(H.L. Clark 1911)	15, 29	8, 26, 45, 69				
		Ophiomyxa		*australis*		Lütken 1869	15, 32, 45	8, 23, 26, 27, 31, 45, 69	13			
		Ophiophrixus		*acanthinus*		H.L. Clark 1911	15, 45	8, 26, 27, 31, 45, 69	33			
		Ophiosmilax		*mirabilis*		Matsumoto 1915		45				
		Ophiostiba		*hidekii*		Matsumoto 1915	32	45				
		Ophiostyracium		*trachyacanthum*		H.L. Clark 1911	45	18				
		Ophiosyzygus		*disacanthus*		H.L. Clark 1911	45	45				
	Ophionereidae	*Ophiocrasis*		*ladens*		Murakami 1944		56				
		Ophiodoris		*percalles*		H.L. Clark 1911	45	45				
		Ophionereis		*dubia*		(Müller & Troschel 1842)	15, 25	23, 26, 31, 45, 69	13, 24			
		Ophionereis		*eurybrachiplax*		H.L. Clark 1911	26	45				
		Ophionereis		*intermedia*		A.M. Clark 1953			13			
		Ophionereis		*porrecta*		Lyman 1860	32, 45	52				
		Ophionereis		*semoni*		(Döderlein 1896)	32		14			
		Ophionereis		*thryptica*		(Murakami 1943)	32		14			
		Ophionereis		*variegata*		Duncan 1879	25	23	14			
	Ophionereididae	*Ophionereis*		*annulosa*		(Leconte 1851)	45					
	Ophiotricidae	*Macrophiothrix*		*belli*		Döderlein 1896	32					
		Macrophiothrix		*demessa*		(Lyman 1861)	32					
		Macrophiothrix		*hirtusa*		(Müller & Troschel 1842)	45					
		Macrophiothrix		*hybrida*		H.L. Clark 1915	15					
		Macrophiothrix		*leucostricha*		(Hoggett 1991)	32					
		Macrophiothrix		*longipeda*		(Lamarck 1816)	25, 32, 45	23, 26, 45, 69				

(continued)

Order	Family	Species					Subtropical	Temperate	Middle temperate	Cool temperate	Subarctic	?
		Macrophiothrix		*nereidina*		(Lamarck 1816)	25, 32, 45	26, 31, 45, 69				
		Macrophiothrix		*obtusa*		Koehler 1905	45					
		Macrophiothrix		*propinqua*		(Lyman 1861)	32					
		Macrophiothrix		*vicina*		(Koehler 1930)	53					
		Ophiogymna		*elegans*		(Ljungman 1866	25	23, 26, 28, 69				
		Ophiogymna		*fulgens*		(Koehler 1905)	15, 25, 29, 32	8, 26, 28, 69	14			
		Ophiogymna		*pellicula*		(Duncan 1879)	28, 45	45				
		Ophiomaza		*cacaotica*		Lyman 1871	25, 32	23, 26, 45, 69	13			
		Ophiothela		*danae*		Verrill 1869	25, 32	23, 26, 31, 45, 69	33			
		Ophiothrix	(*Acanthophiura*)	*purprea*		Martens 1867	25, 32, 55					
		Ophiothrix	(*Ophiothrix*)	*ciliaris*		(Lamarck 1816)	25, 32	23, 26, 45				
		Ophiothrix	(*Ophiothrix*)	*exigua*		Lyman 1874	25, 29, 45	23, 26, 31, 45, 69	10, 13, 24, 45, 47			
		Ophiothrix	(*Ophiothrix*)	*koreana*		Duncan 1879	25, 45	23, 45, 69	24, 45			
		Ophiothrix	(*Ophiothrix*)	*panchyendyta*		H.L. Clark 1911	8, 15, 29	26, 27, 45	7			
		Ophiothrix	(*Ophiothrix*)	*trillineata*		Lütken 1869	32					
		Ophiothrix		*marginata*		Koehler 1905	25					
	Ophiuridae	*Amphiophiura*		*convexa*		Hertz 1927						45
		Amphiophiura		*lapidaria*		(Lyman 1878)		45				
		Amphiophiura		*megapoma*		(H.L. Clark 1911)			45			
		Amphiophiura		*oediplax*		(H.L. Clark 1911)			45			
		Amphiophiura		*penichra*		(H.L. Clark 1911)				28	45	
		Amphiophiura		*pompophora*		(H.L. Clark 1911)	45	45	33			
		Amphiophiura		*sculptilis*		(Lyman 1878)	45	45				
		Amphiophiura		*sculpta*		(Duncan 1879)	45	45				
		Astrophiura		*kawamurai*		Matsumoto 1913		45				
		Astrophiura		*wanikawai*		Fujita & Hendler 2001		11				
		Oophiocten		*hastatum*		Lyman 1878		8	7			

		Ophiochalcis		*scabra*		(Koehler 1905)	15	8	14			
		Ophioplinthus		*clasta*		(H.L. Clark 1911)		45				
		Ophiura		*atacta*		H.L. Clark 1911			17			
		Ophiura		*kinbergi*		Ljungman 1866	15, 25, 32, 45	8, 23, 26, 27, 31, 45, 69	13, 24, 45, 47	17, 36	12	
		Ophiura	(*Ophiuroglypha*)	*irrorata*		(Lyman 1878)	45	45			45	
		Ophiura		*albata*		(Lyman 1878)		45				
		Ophiura		*bathybia*		H.L. Clark 1911			17	17	17	
		Ophiura		*calyptolepis*		H.L. Clark 1911		45				
		Ophiura		*cryptolepis*		H.L. Clark 1911		45	17	17		
		Ophiura		*flagellata*		Lyman 1878	15, 45	8, 26, 27, 45	7, 45			
		Ophiura		*imbecillis*		(Lyman 1878)	45	45, 69				
		Ophiura		*leptoctenia*		H.L.Clark 1911		45	7, 13, 17, 45	17	17, 45	
		Ophiura		*maculata*		Ludwig 1886					45	
		Ophiura		*micracantha*		H.L. Clark 1911	15, 45	45				
		Ophiura		*monostoecha*		H.L. Clark 1911	45	8, 45, 69				
		Ophiura		*ooplax*		H.L. Clark 1911	45	8, 45, 69				
		Ophiura		*paucisquamata*		Matsumoto 1917		26, 45, 69				
		Ophiura		*quadrispina*		H.L. Clark 1911			7, 13, 17, 45	17	17, 45	
		Ophiura		*sarsii*		Lütken 1855	45	27, 45, 69	7, 12, 13, 17, 24, 45, 47	12, 17, 45	12, 17, 45	
		Stegophiura		*brachyactis*		(H.L. Clark 1911)					45	
		Stegophiura		*nodosa*		(Lütken 1855)					45	
		Stegophiura		*ponderosa*		(Lyman 1878)		45			45	
		Stegophiura		*sladeni*		(Duncan 1879)	15, 25, 29, 45	8, 26, 27, 31, 45	7, 13, 45			
		Stegophiura		*sterea*		(H.L. Clark 1908)	25, 45	8, 26, 27, 45, 69	7, 45			
		Stegophiura		*striata*		(Duncan 1879)			33, 45			
		Stegophiura		*vivipara*		Matsumoto 1915	15, 32	8, 26, 31, 45	14			

References

Baker AN (1980) Euryalinid Ophiuroidea (Echinodermata) from Australia, New Zealand, and the South-West Pacific Ocean. NZ J Zool 7:11–83

Baranova ZI (1964) Echinodermata collected during the expedition on ice-breaker “F.Litke” in 1955. Tr Arcticheskogo i Antarcticheskogo Nauchno-Issledovatel’skogo Inst 259:355–372 [in Russian]

Blake DB (2013) Early Asterozoan (Echinodermata) diversification: a paleontologic quandary. J Paleontol 87:353–372

Byrne M (1994) Ophiuroidea. In: Harrison FW, Chia F-S (eds) Echinodermata, vol 14, Microscopic anatomy of invertebrates. Wiley-Liss, New York, pp 247–343

Cannon JT, Kocot KM, Waits DS, Weese DA, Swalla BJ, Santos SR, Halanych KM (2014) Phylogenomic resolution of the hemichordate and echinoderm clade. Curr Biol 24:2827–2832

Clark HL (1908) Some Japanese and East Indian Echinoderms. Bull Mus Comp Zool 51:279–311

Clark HL (1911) North Pacific ophiurans in the collection of the United States National Museum. Smith Inst US Nat Mus Bull 75:1–301

Clark HL (1915) Catalogue of recent ophiurans: based on the collection of the Museum of Comparative Zoölogy. Mem Mus Comp Zool Harv Coll 25:165–376

Dahm C, Brey T (1998) Determination of growth and age of slow growing brittle stars (Echinodermata: Ophiuroidea) from natural growth bands. J Mar Biol Assoc UK 78:941–951

Djakonov AM (1954) Ophiuroids of the USSR seas. In: Pavlovskii EN (ed) Keys to the fauna of the USSR. Wiener Bindery, Jerusalem, pp 1–123

Döderlein L (1902) Japanese Euryalida. Zool Anz 25:320–326 [in German]

Döderlein L (1911) About Japanese and other Euryalids. Abh Bayer Ak Wiss 2:1–123 [in German]

Döderlein L (1927) Indo-Pacific Euryalida. Abh Bayer Ak Wiss 31:1–105 [in German]

Döderlein L (1930) The Ophiuroidea: the German deep-sea expedition. 2. Euryalida. Deut Tiefsee-Exped 1898–1899 22:347–396 [in German]

Emson RH, Woodley JD (1987) Submersible and laboratory observations of *Asteroschema tenue*, a long-armed euryaline brittlestar epizoic on gorgonians. Mar Biol 96:31–45

Fell HB (1962) Evidence for the validity of Matsumoto’s classification of the Ophiuroidea. Publ Seto Mar Biol Lab 10:145–152

Fujikura K, Lindsay D, Kitazato H, Nishida S, Shirayama Y (2010) Marine biodiversity in Japanese waters. PLoS One 5:e11836

Fujita T (1996) Bathymetric distribution of ophiuroids (Echinodermata) off Sendai Bay, Northern Japan, with notes on the diet of the Roughscale Sole *Clidoderma asperrimum* (Pisces, Pleuronectidae). Mem Natl Mus Tokyo 29:209–222

Fujita T (1998) Ophiuroids (Echinodermata) from Fukue Island off Kyushu, Western Japan, including three new records for Japan. Mem Natl Mus Tokyo 31:224–230

Fujita T (2003) Arm regeneration frequency in bathyal populations of *Ophiura sarsii* off Northern Japan. In: Féral J-P, David B (eds) Echinoderm research. Swets & Zeitlinger, Lisse, pp 221–227

Fujita T, Hendler G (2001) Description of a new species of *Astrophiura* (Echinodermata: Ophiuroidea) from Tosa Bay, Japan, and several of its remarkable anatomical characters. Nat Sci Mus Monogr 20:263–281

Fujita T, Irimura S (2005) Ophiuroids (Echinodermata) collected by R/V *Yoko-Maru* off Southwestern Japan in the East China. Nat Sci Mus Monogr 29:357–384

Fujita T, Kohtsuka H (2003) Ophiiuroids (Echinodermata) from Notojima Islands and its adjacent waters in the Sea of Japan. Rep Noto Mar Cent 9:25–38 [in Japanese with English title and abstract]

Fujita T, Ohta S (1990a) Photographic observations of deep-sea infaunal ophiuroids in Suruga Bay, central Japan: an application of a free fall system of time-lapse cameras and current meters. J Oceanogr Soc Japan 46:230–236

Fujita T, Ohta S (1990b) Size structure of dense populations of the brittle star *Ophiura sarsii* (Ophiuroidea: Echinodermata) in the bathyal zone around Japan. Mar Ecol Prog Ser 64:113–122

Fujita T, Saba M (2000) Asteroids and ophiuroids (Echinodermata) collected in the seas around Takehara, Hiroshima Prefecture, Japan. Mem Natl Mus Tokyo 33:167–174

Fujita T, Ishida Y, Irimura S (1997) Ophiuroids collected from the deep waters of Suruga Bay, central Japan. Nat Sci Mus Monogr 12:257–268

Fujita T, Ishida Y, Kato T, Irimura S (2004) Ophiuroids (Echinodermata) collected from the Oki Islands in the Sea of Japan. Bull Natl Sci Mus Ser A Zool 30:191–218

Fujita T, Ishida Y, Irimura S (2006) Preliminary report of Ophiacanthidae (Echinodermata, Ophiuroidea) collected from the Sagami Sea, central Japan. Mem Natl Mus Tokyo 41:289–303

Fujita T, Iwasaki U, Okanishi M (2009) Ophiuroids (Echinodermata) of Genus *Ophiura* collected from deep waters off Pacific Coast of Northern Japan. Nat Sci Mus Monogr 39:619–653

Fujita T, Kawase O, Hendler G (2011) Rediscovery and redescription of a rare brittle star, *Amphiura multispina* (Echinodermata, Ophiuroidea, Amphiuridae). Bull Natl Mus Nat Sci Ser A 37:209–215

Fujita T, Ishida Y, Kogure Y (2014) Ophiuroids (Echinodermata) collected by the R/V *Mizuho-Maru* from the continental shelf in the Sea of Japan. Nat Sci Mus Monogr 44:205–223

Gage JD (1990) Skeletal growth bands in brittle stars: microstructure and significance as age markers. J Mar Biol Assoc UK 70:209–224

Hendler G (1988) Ophiuroid slkeleton ontogeny reveales homologies among skeletal plates of adults: a study of *Amphiura fitiformis*, *Amphiura stimpsonii* and *Ophiophragmus filograneus* (Echinodermata). Biol Bull 174:20–29

Hendler G, Migotto AE, Ventura CRR, Wilk L (2012) Epizoic *Ophiothela* brittle stars have invaded the Atlantic. Coral Reefs 31:1005

Hotchkiss FHC, Glass A (2012) Observations on *Onychaster* Meel & Worthen, 1868 (Ophiuroidea: Onychasterdiae) (Famennian–Visea age). Zoosymposia 7:121–138

Hotchkiss FHC, Prokop RJ, Petr V (1999) Isolated vertebrae of brittle stars of the family Klasmuridae Spencer, 1925 (Echinodermata: Opohiurooidea) in the Devonian of Bohemia (Czech Republic). J Czech Geol Soc 44:319–334

Irimura S (1968a) A new species of Ophiuroidea from the coast of Kii Peninsura, Japan. Publ Mar Biol Lab 15:353–356

Irimura S (1968b) Preliminary report of ophiuroids from Tanabe Bay and adjacent waters. Nanki Seibutu 10:30–38 [in Japanese]

Irimura S (1969) Supplemental report of Dr. Murakami's paper on the ophiurans of Amakusa, Kyushu. Publ Amakusa Mar Biol Lab 2:37–48

Irimura S (1979) Ophiuroidea of Sado Island, the Sea of Japan. Ann Rep Sado Mar Biol Sta Niigata Univ 9:1–6

Irimura S (1981) Ophiurans from Tanabe Bay and its vicinity, with the description of a new species of *Ophiocentrus*. Publ Mar Biol Lab 26:15–49

Irimura S (1982) The brittle-stars of Sagami Bay: collected by his Majesty the Emperor of Japan. Biol Lab Imp Household, Tokyo, pp 1–95

Irimura S (1990) Ophiuroidea. In: Japan Fisheries Resource Conservation Association (ed) Echinoderms from continental shelf and slope around Japan, vol 1. Tosho Printing, Tokyo, pp 65–100

Irimura S (1991) Ophiuroidea. In: Japan Fisheries Resource Conservation Association (ed) Echinoderms from continental shelf and slope around Japan, vol 2. Tosho Printing, Tokyo, pp 111–152

Irimura S, Kubodera T (1998) Ophiuroidea in the East China Sea. Mem Natl Sci Mus Tokyo 30:135–143

Irimura S, Tachikawa T (2002) Ophiuroids from the Ogasawara Islands (Echinodermata: Ophiuroidea). Ogasawara Res 28:1–27

Irimura S, Yoshino H (1999) *Ophioplocus giganteus*, a new species of Ophiuroidea from Okinawa Island, Southwestern Japan. Bull Nat Sci Mus Ser A Zool 25:143–148

Irimura S, Fujita T, Ueshima R (2001) Preliminary report on the Ophiuroids (Echinodermata) on the shelf off Shimoda, south of Izu Peninsula, central Japan. Mem Natl Sci Mus Tokyo 37:311–315 [in Japanese with English Abstract]

Ishida Y, Ohtsuka S, Takayasu K, Kobayashi I, Lee Y, Seto K, Tanaka H, Tamura K, Go A, Nakaguchi K (2001) Preliminary faunistic survey of Ophiuroids in the westernmost parts of the Sea of Japan. J Fac Appl Biol Sci 40:1–14

Jangoux M, Ridder CD, Fecher H (1987) Annotated catalogue of recent echinoderm type specimens in the collection of the Zoologische Staatssammlung München (Echinodermata). Spixiana 10:295–311

Janies DA, Voight JR, Daly M (2011) Echinoderm phylogeny including *Xyloplax*, a progenetic asteroid. Syst Biol 60:420–438

Koehler R (1907) Revision de la collection des Ophiures du Museum de Paris. Bull Sci Fra Belg 41:279–352

Komatsu M, Shibata D, Wakabayashi K, Kogure Y, Kano Y, Takahashi N (2007) Echinoderms in the littoral region of Rishiri Island. Rishiri Stud 26:1–14 [in Japanese with English title and abstract]

Littlewood DTJ, Smith AB, Clough KA, Emson RH (1997) The interrelationships of the echinoderm classes: morphological and molecular evidence. Biol J Linn Soc Lond 61:409–438

Litvinova NM (1989a) Ecological interpretation of the structural characters in brittle star arms. 2. Variability and functional morphology of vertebral joints in arms. Zool Zh 68:41–55 [in Russian with English title and abstract]

Litvinova NM (1989b) Ecological interpretation of the structural characters in brittle star arms. 1. Variability in shapes of arm vertebrae. Zool Zh 68:97–195 [in Russian with English title and abstract]

Litvinova NM (1996) Ecological interpretation of structural characteristics of brittle stars arms. 3. Arm forms and external skeletons (integuments). Zool Zh 75:1676–1689 [In Russian with English title and abstract]

Lyman T (1879) Ophiuridae and Astrophytidae of the exploring voyage of H. M. S. "Challenger," under Prof. Sir Wyville Thomson, F.R.S. Bull Mus Comp Zool Harv Coll Camb 6:217–238

Lyman T (1882) Report on the Ophiuroidea. Rep Sci Challenger Zool 5:1–386

Martynov A (2010) Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae. Zootaxa 2697:1–154

Matsumoto H (1911) About a family of Euryalida in Japan. Dobutsugaku-zasshi 23(277):617–631 [in Japanese]

Matsumoto H (1912a) About family Gorgonocephalidae in Japan. Dobutsugaku-zasshi 24 (282):198–206 [n Japanese]

Matsumoto H (1912b) Revision of orders in recent Ophiuroids. Dobutsugaku-zasshi 24 (283):263–269 [in Japanese]

Matsumoto H (1912c) Revision of Euryalida in Japan. Dobutsugaku-zasshi 24(285):379–390 [in Japanese]

Matsumoto H (1912d) Notes on *Asteronyx loveni*. Dobutugaku-zasshi 24(288):588–590 [in Japanese]

Matsumoto H (1915) A new classification of the Ophiuroidea: with descriptions of new genera and species. Proc Acad Nat Sci Phila 67:43–92

Matsumoto H (1917) A monograph of Japanese Ophiuroidea, arranged according to a new classification. J Coll Sci Imp Univ Tokyo 38:1–408

Matsumoto H (1918) On a collection of ophiurans from Kinkwasan. Annot Zool Jpn 9:475–480

Matsumoto H (1941) Report of the biological survey of Mutsu Bay 36. Ophiuroidea of the Mutsu Bay and vicinities. Sci Rep Tohoku Imp Univ 16:331–344

McKnight DG (2000) The marine fauna of New Zealand: basket-stars and snake-stars (Echinodermata: Ophiuroidea: Euryalinida). Nat Inst Water Atmos Res Biodivers Mem 115:1–79

Mortensen T (1911) *Astroclon suensoni* n. sp. A new East Asiatic euryalid. Vidensk Medd Dansk Nat Fore Kjøbenhaven 63:209–212

Mortensen T (1927) Handbook of the echinoderms of the British Isles. Oxford University Press, London, pp 1–471

Mortensen T (1933) Studies of Indo-Pacific euryalids. Vidensk Medd Dansk Nat Fore Kjøbenhaven 96:1–75

Murakami S (1942) Ophiurans of Izu, Japan. J Dep Agric Kyusyu Imp Univ 7:1–36

Murakami S (1943a) Report on the ophiurans of Palao, Caroline Islands. J Dep Agric Kyusyu Imp Univ 7:159–204

Murakami S (1943b) Report on the ophiurans of Yaeyama, Ryu-Kyu. J Dep Agric Kyusyu Imp Univ 7:205–222

Murakami S (1943c) Ophiurans from some gulfs and bays of Nippon. J Dep Agric Kyusyu Imp Univ 7:223–234

Murakami S (1944a) Report on the ophiurans from Ogasawara Islands and from off the Yeayama group, Nippon. J Dep Agric Kyushu Imp Univ 7:235–257

Murakami S (1944b) Note on the ophiurans of Amakusa, Kyusyu. J Dep Agric Kyusyu Imp Univ 7:259–280

Murakami S (1963a) On some ophiurans from Kii and vicinities with descriptions of a new species. Publ Seto Mar Biol Lab 11:171–184

Murakami S (1963b) The dental and oral plates of Ophiuroidea. Trans R Soc NZ 4:1–47

Nishimura S (1981) Ocean and life on the earth. Introduction to marine biogeography. Kaimeisha, Tokyo [in Japanese]

Nomura K (1993) Shallow-water Ophiuroidea of Akajima Island, Kerama Group, Ryukyu Island. Midori-ishi 4:23–27 [in Japanese]

O'Hara TD, Hugall AF, Thuy B, Moussalli A (2014) Phylogenomic resolution of the class Ophiuroidea unlocks a global microfossil record. Curr Biol 24:1874–1879

Okanishi M, Fujita T (2009) A new species of *Asteroschema* (Echinodermata: Ophiuroidea: Asteroschematidae) from Southwestern Japan. Species Divers 14:115–129

Okanishi M, Fujita T (2011a) Two new species of the subgenus *Asteroporpa* (*Astromoana*) (Ophiuroidea: Euryalida: Gorgonocephalidae) from Japan. Zootaxa 2751:25–39

Okanishi M, Fujita T (2011b) A taxonomic review of the genus *Astrocharis* Koehler (Echinodermata: Ophiuroidea: Asteroschematidae) with a description of a new species. Zool Sci 28:148–157

Okanishi M, Fujita T (2013) Molecular phylogeny based on increased number of species and genes revealed more robust family-level systematics of the order Euryalida (Echinodermata: Ophiuroidea). Mol Phylogenet Evol 69:566–580

Okanishi M, Fujita T (2014a) A taxonomic review of the genus *Astrodia* (Echinodermata: Ophiuroidea: Asteronychidae). J Mar Biol Assoc UK 91:187–201

Okanishi M, Fujita T (2014b) A taxonomic review of the genus *Asterostegus* (Echinodermata: Ophiuroidea), with the description of a new species. Eur J Taxon 76:1–18

Okanishi M, Yamaguchi K, Horii Y, Fujita T (2011a) Ophiuroids of the order Euryalida (Echinodermata) from Hachijo-jima Islnad and Ogasawara Islands, Japan. Mem Natl Mus Nat Sci 47:367–385

Okanishi M, O'Hara D, Fujita T (2011b) Molecular phylogeny of the order Euryalida (Echinodermata: Ophiuroidea), based on mitochondrial and nuclear genes. Mol Phylogenet Evol 61:392–399

Okanishi M, O'Hara D, Fujita T (2011c) A new genus *Squamophis* of Asteroschematidae (Echinodermata: Ophiuroidea: Euryalida) from Australia. ZooKeys 129:1–15

Okanishi M, Tachinkawa H, Fujita T (2011d) *Astrochele pacifica* Mortensen, 1933 (Echinodermata: Ophiuroidea: Euryalida: Gorgonocephalidae) obtained from Katsuura, Chiba, Japan. J Nat Hist Mus Inst Chiba Spec Issue 9:97–102

Okanishi M, Olbers JM, Fujita T (2013) A taxonomic review of the genus *Asteromorpha* (Echinodermata: Ophiuroidea: Euryalidae). Raffles Bull Zool 61:461–480

Okanishi M, Moritaki T, Fujita T (2014) Redescription of an euryalid bittle star, *Astroceras coniunctum* (Echinodermata: Ophiuroidea: Euryalidae). Bull Natl Mus Nat Sci Ser A Zool 40:133–139

Parameswaran UV, Jaleel AKU (2012) *Asteroschema sampadae* (Ophiuroidea: Asteroschemetinae), a new deep-sea brittle star from the continental slope off the southern tip of India. Zootaxa 3269:47–56

Perseke M, Bernhard D, Fritzsch G, Brümmer F, Stadler PF, Schlegel M (2010) Mitochondrial genome evolution in Ophiuroidea, Echinoidea, and Holothuroidea: insights in phylogenetic relationships of Echinodermata. Mol Phylogenet Evol 56:201–211

Rho BJ, Kim HS (1966) Studies on the Echinodermata (Echinodeidea, Asteroidea and Ophiuroidea) from Korea. Collect Thes Writ Commen Dr. Emma Kim's Forty years Trac Ewha Womens Univ Seoul, Korea, pp 273–293

Rho BJ, Shin S (1983) A systematic study on the Ophiuroidea in Korea. 2. J Korean Res Inst Bet Liv Ewha Womans Univ 31:57–64

Rho BJ, Shin S (1987) Systematic study on the Ophiuroidea from Cheju Island, Korea. Korean J Syst Zool 3:208–224

Rowe FEW, Gates J (1995) Echinodermata. In: Wells A (ed) Zoological catalogue of Australia, vol 33. CSIRO, Melbourne, pp 1–510

Saba M, Tomida Y, Kimoto T (1982) Echinoderms fauna of Ise Bay, and the northern and the middle parts of Kumano-nada. Bull Mie Pref Mus Nat 4:1–82 [in Japanese]

Shin S, Rho BJ (1996) [Illustrated encyclopedia of fauna and flora of Korea. 36. Echinodermata]. Ministry of Education, Seoul, pp 1–175 [in Korean]

Smith AB, Paterson GLJ, Lafay B (1995) Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. Zool J Linn Soc 114:213–243

Spencer WK, Wright CW (1966) Asterozoa. In: Moore RC (ed) Treatise on invertebrate paleontology, Part U. Echinodermata 3. Geological Society of America and University of Kansas Press, Lawrence, pp U4–U107

Stöhr S (2011) New records and new species of Ophiuroidea (Echinodermata) from Lifou, Loyalty Islands, New Caledonia. Zootaxa 3089:1–50

Stöhr S, O'Hara T, Thuy B (2012) Global diversity of brittle stars (Echinodermata: Ophiuroidea). PLoS One 7:e31940

Stöhr S, O'Hara T, Thuy B (eds) (2014) World Ophiuroidea database. Available at http://www.marinespecies.org/ophiuroidea on 10 Dec 2014

Tajiri R, Fujita T (2013) Observation methods of hard and soft tissues by grinding specimens impregnated with resin. Taxa 35:24–34 [in Japanese with English title and abstract]

Telford MJ, Lowe CJ, Cameron CB, Ortega-Martinez O, Aronowicz J, Oliveri P, Copley RR (2014) Phylogenomic analysis of echinoderm class relationships supports Asterozoa. Proc Biol Sci 281:doi:10.1098/rspb.2014.0479

Thuy B, Stöhr S (2011) Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropalaeontology and classification. Zootaxa 3013:1–47

Verrill AE (1869) New and imperfectly known echinoderms and corals. Proc Boston Soc Nat Hist 12:381–396

Verrill AE (1899) Report on the Ophiuroidea collected by the Bahama expedition in 1893. Bull Lab Nat Hist State Univ Iowa 5:1–86

Wilding TA, Gage JD (1995) Skeletal growth marks in the brittle star *Ophiura ophiura* (Linnaeus): do they reflect a seasonal growth pattern? In: Emson R, Smith A, Campbell A et al (eds) Echinoderm research. Balkema, Rotterdam, pp 283–291

Chapter 26
Taxonomy of Ascidians (Urochordata: Ascidiacea) in Japan: Past, Present, and Future

Teruaki Nishikawa

Abstract A historical retrospect of the ascidian taxonomy in Japan is briefly given, with a taxonomic revision of Hartmeyer's (Zool Anz 31:1–30, 1906) monograph based on my reexamination of name-bearing type and other specimens long kept in European museums. The revision includes a new proposal of *Styela elsa* Hartmeyer, 1906 as a junior synonym of *Styela fertilis* Hartmeyer, 1906, correcting Nishikawa's (Publ Seto Mar Biol Lab 35:99–103, 1991) nomenclatural act on *S. elsa* as a junior synonym of *S. clara* Hartmeyer, 1906, because of the rediscovery in 1998 of a syntype of *S. elsa*. Recent advances in our understanding of ascidian diversity in Japanese waters are exemplified by the studies on *Halocynthia roretzi* and *Halocynthia hilgendorfi* species complexes and the photosymbiotic species of the family Didemnidae. Also mentioned in this chapter are the seven alien ascidians so far known from Japanese coasts, as *Molgula manhattensis* since 1972, *Polyandrocarpa zorritensis* since 1991, *Phallusia philippinensis* in the sense of Vandepas and others since 1999 or earlier, *Microcosmus squamiger* since 2007, *Ascidiella aspersa* since 2008, the Atlantic form of *Clavelina lepadiformis* complex since 2011, and *Microcosmus exasperatus* since 2014.Abstract citations have been replaced with complete reference details. Please check and confirm.I have checked the citations. Thank you.

Keywords Morphology • Molecular phylogenetics • Alien • Name-bearing type • Museum • Life history • Nomenclature • Synonymy

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26.1 Introduction

Urochordata (or Tunicata, ranked here at the phylum level following Satoh et al. 2014), are exclusively marine invertebrate chordates, and now regarded as the closest relatives of vertebrates, in place of cephalochordates (lancelets), based on recent results of molecular phylogenetics and comparative genomics. Urochordates include approximately 3000 known extant species (see Shenker and Swalla 2011), traditionally classified into three classes, Appendicularia (larvaceans, ~70 known species), Ascidiacea (sea squirts or ascidians, more than 2800 known species, with two orders Enterogona and Pleurogona), and Thaliacea (salps, doliolids, and pyrosomes, ~70 known species), each with a distinct morphology and a life history. Appendicularians and thaliaceans are holoplanktonic, whereas ascidians almost always have a very short pelagic duration of lecithotrophic larvae, followed by settlement and metamorphosis into the sessile adult form.

This classification has been challenged by molecular phylogenetic analyses since Wada's (1998) first claim for the ascidian paraphyly using the 18S rRNA gene. Now in terms of molecular information, the two orders of Ascidiacea, that is, Enterogona and Pleurogona, are likely sister to Thaliacea and Appendicularia, respectively (Yokobori et al. 2006; Tsagkogeorga et al. 2009), suggesting the ascidian non-monophyly. On the other hand, urochordates as a whole have been unanimously proved monophyletic. In a traditional system (Nishikawa 2000), Enterogona consists of the suborders Aplousobranchia (including Polyclinidae, Didemnidae, and Polycitoridae) and Phlebobranchia (Cionidae, Perophoridae, Ascidiidae, Plurellidae, Agnezidae, Corellidae, and Octacnemidae), and Pleurogona consists of the suborders Stolidobranchia (Botryllidae, Styelidae, Pyuridae, Molgulidae) and Aspiraculata (Hexacrobyliodae). Hexacrobylidae, a deep-water carnivorous family, was sometimes included in the class Sorberacea, distinct from the class Ascidiacea, since Monniot et al. (1975); however, Tatián et al. (2011) recently claimed using molecular markers that Sorberacea or Hexacrobylidae should be abolished to be amalgamated into Molgulidae. Another deep-water family with highly modified pharynx and often carnivorous mode of feeding, Octacnemidae, was safely included in Phlebobranchia, akin to Corellidae, by the Kurabayashi et al. (2003) molecular analyses. In spite of possible non-monophyly of Ascidiacea as just shown, its two halves (Enterogona and Pleurogona) are treated altogether in this chapter.

For species richness in the Japanese ascidian fauna, as Tokioka (1963) shows, its first comprehensive review was made by Hartmeyer (1906; see Table 26.1) who referred to 43 species including many new ones, and then by Oka (1935b), who recorded 106 species at the final work summing up his ascidian studies of about 40 years. After about 30 years, the ascidian fauna of Japan and vicinity was estimated by Tokioka (1963) to constitute approximately 300 taxa of species group rank. Nishikawa (1990, 1991, 1992) reviewed the ascidian fauna of the Sea of Japan, reporting that it consisted of 158 taxa of species group rank, with some taxonomic revisions resulted from his own reexaminations of many name-bearing type specimens or other old museum specimens used by Hartmeyer, Oka, and Tokioka; the results were incorporated into Nishikawa's (1995) summary. Needless

Table 26.1 A taxonomic revision of Hartmeyer's (1906) paper on Japanese ascidians on the basis of Nishikawa's (1991, 2002a, unpublished) reexaminations of name-bearing type or other specimens, arranged in order of appearance in Hartmeyer's

Hartmeyer's original name	Valid name	Japanese name	Registration number	Status	Locality (depth)	Collector	Invalidated name	Remarks and references
Molgula japonica n.sp.	*Molgula japonica* Hartmeyer, 1906		ZMB1115	Holotype	Yokohama	D'Arcy W. Thompson		The holotype is similar to *M. hartmeyeri* Oka, 1914, but further consideration will be given elsewhere; collector's name added from the label information
Microcosmus polymorphus Heller	*Microcosmus hartmeyeri* Oka, 1906	Haruto-boya	ZSM5301		Ito, Sagami Bay	Haberer		ZSM specimens are not included in Nishikawa (1991:149–151)
			ZSM9285		Fukuura, Sagami Bay	Haberer		
			missing		Jogashima, Sagami Bay (150 m)	Doflein		
Halocynthia pallida (Heller)	*Herdmania japonica* (Hartmeyer, 1909)		ZMB2802	Syntypes (part)	Tokyo Bay, 600 m	Doflein		Nishikawa (2002a)
Halocynthia sanderi (Traust. u. Weltn.) und Verwandte	*Pyura sacciformis* (von Drasche, 1884)	Mihaeru-boya	ZMB2226		Miyatsu, Wakasa Bay (70 m)	Döderlein	*Cynthia japonica* Traustedt, 1885; *C. sanderi* Traustedt and Weltner, 1894; *Halocynthia michaelseni* Oka, 1906; *H. jokoboja* Oka, 1906; *H. hystrix* Oka, 1930; *Pyura aspera* Tokioka, 1949; *P. masuii* Tokioka, 1949	Not included in Nishikawa (1980, 1991); the holotype of *P. sacciformis* is registered NHMW-Mollusca IN 74666; the syntypes of *C. sanderi* are registered ZMB382 (from Nagasaki) and ZMB383 (from Yokohama); the holotype of *C. japonica* is deposited in UZMK without registration number (see Nishikawa 1991:131)
			ZMB2227		Tanagawa, Osaka Bay (~30 m)	Döderlein		
			ZMB1050		Nagasaki	Schottmüller		
			ZSM935		Near Misaki, Sagami Bay	Doflein		
			ZSM 942 (part)		Miura Pen., Sagami Bay	Doflein		
			ZMB57[a]		Yokohama	Martens		

(continued)

Table 26.1 (continued)

Hartmeyer's original name	Valid name	Japanese name	Registration number	Status	Locality (depth)	Collector	Invalidated name	Remarks and references
Halocynthia comma n. sp.	*Pyura comma* (Hartmeyer, 1906)		Missing	Holotype	Near Misaki, Sagami Bay (180 m)	Doflein		Newly collected in 2001 (Nishikawa 2006)
Halocynthia roretzi (Drasche)	*Halocynthia roretzi* (von Drasche, 1884) species complex	"Ma-boya"	ZSM923		Near Misaki, Sagami Bay	Doflein	ZMB27 is documented in the catalogue, with specimens unavailable	The holotype is registered NHMW-Mollusca IN 101017; for taxonomy of this species complex see Nishikawa (1999a) and the present text
			ZMB27 (missing)		Tokyo Bay	Martens		
			ZMB595^{a}		Hakodate	Doflein		
Halocynthia hildendorfi (Traust.)	*Halocynthia hildendorfi* (Traustedt, 1885)	Iga-boya	ZSM946		Onagawa, Tohoku District	Doflein		Part of *Halocynthia hispida* (Herdman, 1881) in the sense of Nishikawa (1995), distinct from *H. ritteri* Oka, 1906; for details see Nishikawa (1999a) and the present text
			ZMB594^{a}	Syntypes	Hakodate, Hokkaido	Hilgendorf		
Halocynthia arctica (Hartmr.)?	? *Boltenia echinata iburi* (Oka, 1934)	?Iburi-toge-kushiera-boja	ZMB1091		Hakodate, Hokkaido	Hilgendorf		Labeled "*Boltenia echinata* (L.)"; detailed examination impossible because of injury of mantle body
Styela irene n. sp.	*Cnemidocarpa irene* (Hartmeyer, 1906)	Shiroboya-modoki	ZMB2230	Holotype	Miyatsu, Wakasa Bay (70–80 m)	Döderlein	*C. valborg* Hartmeyer, 1919; *Styela esther* Hartmeyer, 1906	Nishikawa (1991:96–99); distinct from *C. areolata* (Heller, 1878)
Styela esther n. sp.	*Cnemidocarpa irene* (Hartmeyer, 1906)	Shiroboya-modoki	ZMB2799	Syntype (part)	Fukuura, Sagami Bay	Haberer		Nishikawa (1991:96–99); *S. esther* sensu Tokioka (1953), is now called *S. tokiokai* Nishikawa, 1991

Styela fertilis n. sp.	*Cnemidocarpa fertilis fertilis* (Hartmeyer, 1906)	Hoso-suji-boya	ZMB2800	Syntype	Tokyo Bay (20 m)	Doflein	*Styela elsa* Hartmeyer, 1906; New synonymy	Nishikawa 1991:103–105, where ZSM943 and 5304 are not included; for the new synonymy see below and the present text
			ZSM943 (part)	Syntype	Uraga Channel (80 m)	Doflein		
			ZSM5304	Syntype	Ito, Sagami Bay	Haberer		
Styela elsa n. sp.	ZSM924: *Cnemidocarpa fertilis fertilis* (Hartmeyer, 1906)	Hoso-suji-boja	ZSM924	Lectotype	Okinose, Sagami Bay (300 ftms)	Doflein		ZSM924 was unavailable in Nishikawa (1991:101); for the lectotype and paralectotype designation see the text
	ZMB2231: *Cnemidocarpa clara* (Hartmeyer, 1906)	Makuwa-boya	ZMB2231	Paralectotype	Tanagawa, Osaka Bay (~30 m)	Döderlein		
Styela sigma n. sp.	*Styela sigma* Hartmeyer, 1906	Wadatsumi-suchiera	ZMB2801 and ZSM6964 (part)	Syntypes (part)	Dogetsuba, Sagami Bay	Doflein (Owston)		Distinct from *S. atlantica* (Van Name, 1912); ZSM6964 is not included in Nishikawa (1991:123–125)
Styela clara n. sp.	*Cnemidocarpa clara* (Hartmeyer, 1906)	Makuwa-boja	ZMB1092	Syntypes	Hakodate, Hokkaido	Hilgendorf	*Styela macrogastra* Oka, 1935; *Azygocarpa mutuensis* Oka, 1932	Nishikawa (1991:99–103); *Styela elsa* Hartmeyer, 1906 should be excluded from the synonymy of *C. clara*
Styela plicata (Les.)	*Styela plicata* (Lesueur, 1823)	Shiro-boya	ZSM9282		Yokohama	Haberer		ZMB384 was described by Traustedt and Weltner (1894)
			ZMB384[a]		Yokohama	Sander		
Styela clava Herdm.	*Styela clava* Herdman, 1881	E-boya	ZMB2228		Miyatsu, Wakasa Bay (ca. 70 m)	Döderlein		Not included in Nishikawa (1991:114–116)
			ZMB2229		Tanagawa, Osaka Bay (~30 m)	Döderlein		

(continued)

Table 26.1 (continued)

Hartmeyer's original name	Valid name	Japanese name	Registration number	Status	Locality (depth)	Collector	Invalidated name	Remarks and references
Styela longitubis Traust.und Weltn.	*Styela canopus* Savigny, 1816	Futa-suji-boya	ZMB385	Holotype	Yokohama	Sander		New synonymy based on my reexamination of ZMB385; *S. longitubis* was established by Traustedt and Weltner (1894)
Polycarpa döderleini n. sp.	*Polycarpa doederleini* Hartmeyer, 1906		ZMB2232	Syntypes	Sagami Bay (100–200 m)	Döderlein		Nishikawa (1991:89–92)
Polycarpa cryptocarpa (Sluit.)	*Polycarpa cryptocarpa kroboja* (Oka, 1906)	Kuro-boya	Missing		Ito, Sagami Bay	Haberer		Not included in Nishikawa (1991:87–89); this species needs taxonomic revision
			ZSM933		Near Jogashima, Sagami Bay	Doflein		
			ZMB2234		Enoshima, Sagami Bay	Döderlein		
Polycarpa maculata n. sp.	*Polycarpa maculata* Hartmeyer, 1906		ZMB2233	Holotype	Wakasa Bay (80 m)	Döderlein		Not included in Nishikawa (1991:93–94)
Ascidia armata n. sp.	*Ascidia armata* Hartmeyer, 1906		ZSM4896, ZSM5307 and ZMB2803	Syntypes	Ito, Sagami Bay	Haberer		Not included in Nishikawa (1991:49–51)
			Missing	Syntype	Aburatsubo, Sagami Bay	Doflein		
			ZSM936	Syntype	Sagami Bay (110 m)	Doflein		
Ascidia longistriata n. sp.	*Ascidia longistriata* Hartmeyer, 1906		ZSM928	Holotype	Misaki, Sagami Bay	Doflein		Not included in Nishikawa (1991:47–49)

Ascidia divisa Sluit.	*Ascidia sydneiensis* Stimpson, 1885	Sujikire-boya	ZMB2806 and ZSM5300		Ito, Sagami Bay	Haberer	Not listed for future taxonomic revision	Not included in Nishikawa (1991:38–40); this species needs taxonomic revision
			ZMB2805 and ZSM944, 945		Onagawa Bay, Tohoku District	Doflein		
			ZMB2804		Tokyo Bay (20 m)	Doflein		
			ZMB1093		Hakodate, Hokkaido	Hilgendorf		
			ZMB1052		Nagasaki	Schottmüller		
Ascidia granosa Sluit.	*Microgastra granosa* (Sluiter, 1904)	Uzumi-boya	Missing		Near Misaki, Sagami Bay (180 m)	Doflein	*Ascidia* (?) *enigmatica* Nishikawa 1986	ZMB1103 material was reexamined by Nishikawa (1986:177–181)
			ZMB1103		Hakodate	Hilgendorf		
Ascidiella virginea (Müller)	*Ascidiella scabra* (Müller)		ZMB1051		Nagasaki	Schottmüller		Distinct from *A. aspersa* (Müller) (see Nishikawa et al. 2014); ZMB1051 material was reexamined by Nishikawa and Otani (2004), regarding the material as an ephemeral occurrence of alien species
Chelyosoma sibogae Sluit.	*Chelyosoma sibogae* Sluiter, 1904	Kamenoko-boya	ZMB2235		Sagami Bay (ca. 200 m)	Döderlein		Not included in Nishikawa (1991:67–69)
Chelyosoma dofleini n. sp.	*Chelyosoma dofleini* Hartmeyer, 1906	Dofurain-kamenoko-boya	ZSM948	Holotype	Near Misaki, Sagami Bay (350 m)	Doflein		Not included in Nishikawa (1991:69–70)

(continued)

Table 26.1 (continued)

Hartmeyer's original name	Valid name	Japanese name	Registration number	Status	Locality (depth)	Collector	Invalidated name	Remarks and references
Corella japonica Herdm.	*Corella japonica* Herdman, 1880	Doro-boya	ZMB2238		Tokyo Bay	Döderlein	*Corella japonica* var. *asamusi* Oka, 1931	Not included in Nishikawa (1991:63–67); specimens of *C. japonica* collected by Sander from Yokohama and described by Traustedt and Weltner (1894) are registered as ZMB388 and ZMH408
			ZMB2237		Miyatsu, Wakasa Ba (70–80 m)	Döderlein		
			ZSM925		Onagawa Bay, Tohoku District (5–10 m)	Doflein		
			ZSM950		Tokyo Bay (20 m)	Doflein		
Rhodosoma papillosum (Stimps.)	*Rhodosoma turcicum* (Savigny, 1816)	Gamaguchi-boya	ZMB2236		Tokyo Bay	Döderlein		Not included in Nishikawa (1991:61–63)
			Missing		Sagami Bay (110 m)	Doflein		
			ZSM943 (part)		Uraga Channel (80 m)	Doflein		
Ciona intestinalis (L.)	*Ciona intestinalis* (Linnaeus, 1767) species complex (probably sp. A)	Kata-yurei-boya	ZSM9280, 9281		Yokohama, Tokyo Bay	Haberer		Not included in Hoshino and Nishikawa (1985), Nishikawa (1991:32–33); they probably belong to the species A of the complex (for further details see Nishikawa 2012)
			Missing		Yokohama Harbor	Doflein		
			ZMB1201[a]		Hakodate	Hilgendorf		
			ZMB2240[a]		Miyatsu, Wakasa Bay (10 m)	Döderlein		
Ciona indica Sluit.	*Rhopalaea* sp.		ZSM (no number)		Ito, Sagmi Bay	Haberer		Not included in Hoshino and Nishikawa (1985)
Rhopalopsis defecta Sluit.	*Rhopalaea* sp.		ZMB2239		Enoshima, Sagami Bay (ca. 200 m)	Döderlein		Identified with *R. crassa* (Herdman, 1880) by Nishikawa (1991:25–30); this species needs taxonomic revision

Sarcodidemnoides misakiense	*Didemnum misakiense* (Oka and Willey, 1892)	Chibusa-boya	ZSM942 (part)		Miura Pen., Sagami Bay	Doflein		
Macroclinum sp.	*Syndiazona grandis* Oka, 1926	Bozu-boya	ZSM934		Near Jogashima, Sagami Bay (150 m)	Doflein		Not included in Nishikawa (1991:30–31)
			ZSM (no number)[a]		Abratsubo, Sagami Bay	Doflein		
Botrylloides sp.			Missing		Hakodate, Hokkaido	Döderlein		
Leptoclinum sp.			Missing		Hakodate, Hokkaido	Döderlein		
Leptoclinum sp.			Missing		Nagasaki	Döderlein		
Botryllus sp.			Missing		Yokohama, Tokyo Bay	Döderlein		
Distaplia sp.	*Distaplia dubia* (Oka, 1927)		ZMB1110		Yokohama	Sander		Not mentioned in Traustedt and Weltner (1894)
Amaroucium sp.			Missing		Sagami Bay	Döderlein		

NHMW Naturhistorisches Museum Wien, *UZMK* Universitetes Zoologiske Museum København, *ZMB* Museum für Naturkunde in Berlin, *ZMH* Zoologisches Museum, Universität Hamburg, *ZSM* Zoologische Staatssammlung München

[a] Not mentioned in Hartmeyer (1906)

to say, however, the fauna still awaits further taxonomic revisions using molecular and morphological information.

The present chapter aims to somewhat contribute to such revisions expected in the near future. Presented here are our advanced or revised understanding of the Japanese ascidian fauna after Nishikawa (1995), especially in didemnids by Prof. Euichi Hirose of the University of the Ryukyus and his collaborators, with a brief summary of the present knowledge about alien ascidians in Japan.

26.2 Short History of Ascidian Taxonomy in Japan and the Specimens Used

'Hoya' in Japanese has been used to refer usually to the simple ascidian *Halocynthia roretzi* (von Drasche, 1884), now having the Japanese common name 'maboya' (phonological transformation of 'ma-hoya', meaning 'true ascidian'), or possibly to simple ascidians as a whole, since the late seventh century A.D. This name has been exemplified by excavated wooden tablets ('mokkan'; Nara National Research Institute for Cultural Properties 2015), attached to parcels transported as taxes to Fujiwara- and Heian-kyō, Imperial capitals of Japan at that time (now Nara Prefecture); during this era, 'hoya' used to be carried in a fermented form for imperial court cuisine. Long afterward, natural history literature in the Edo period often includes external drawings of 'hoya' readily identifiable as this species. It is often said that 'hoya' may have been coined from a very old Japanese word 'hoya' meaning the mistletoe (a plant parasitic to other trees) because of a similar appearance between mistletoe roots and tunic rooting processes of *H. roretzi* for attachment.

Among the oldest and still available museum specimens of Japanese ascidians are doubtlessly the two yet undescribed ascidians in the von Siebold collection at the Rijksmuseum van Natuurlijke Historie, Leiden (or Naturalis today), made during his stay in Japan from 1823 to 1829 in the late Edo period. The specimens were introduced for the first time as a simple and a compound ascidian by Yamaguchi (1987), with his photographs of Pl-D-3-F-6 and -11, respectively, and the former may seem to belong to *H. roretzi*, although I have not yet examined it. Natural history studies in Japan's Edo period are thought to have been carried out enthusiastically, but had in most cases no special intention to officially keep the studied specimens for future usage, unfortunately. Afterward, the collections of modern taxonomists, Oka, Nishikawa, and Tokioka are largely available in the National Museum of Nature and Science, Tsukuba (for the former two), or at the Seto Marine Biological Laboratory, Kyoto University (for the last two; for a list of the type specimens there see Harada 1991).

The Japanese ascidian fauna was described in the modern sense initially by foreign taxonomists, such as Herdman (1882, 1886) based on the HMS *Challenger* collection in 1875, as well as von Drasche (1884), Traustedt (1885), and Hartmeyer

Fig. 26.1 Color plate in the original description of *Didemnum misakiense* (Oka and Willey 1892), to show a living colony "hanging downwards from the lower surface of the shelving rocks" in the intertidal zone of Moroiso, Sagami Bay, Japan, drawn "by a Japanese artist" (Oka and Willey 1892). Downloaded as "quarterlyjournalplates339192lond_0045 jpg at http://www.biodiversitylibrary.org/item/49107#page/45/mode/1up

(1906) for materials collected by foreign professors or naturalists staying in Japan in the early Meiji period (Roretz, Döderlein, Haberer, Hilgendorf, Doflein, Owston, etc.); their materials are largely still available, as shown in the following section '26.3 Revision of Hartmeyer's. . .' and Table 26.1. The binomina *Diplosoma mitsukurii* Oka, 1892 (Japanese name: nen'eki-boya) and *Didemnum misakiense* (Oka and Wiley, 1892) (chibusa-boya; Fig. 26.1) are the first for a Japanese (Asajiro Oka) to establish (see Oka 1892; Oka and Wiley 1892). Since then, Dr Asajiro Oka, Professor of the Tokyo Higher Normal School (a predecessor of the University of Tsukuba) established many new species in his approximately 55 papers including Oka (1906, 1914, 1935a). The Oka collection has been partly used for taxonomic revision by Tokioka (1954; etc.) and Nishikawa (1981, 1990, 1991; etc.), and its thorough taxonomic revision is now in preparation.

The second Japanese taxonomist is Prof. Takasi Tokioka of the Seto Marine Biological Laboratory, Kyoto University (for his biography see Nishikawa 2002b, c). He was a student of Prof. Taku Komai of Kyoto University, a talented taxonomist and a famous geneticist, and Komai was once taught by Oka. Thus, Tokioka was a pupil of a pupil of Oka. Tokioka, my teacher, published about 60 papers on ascidians, including voluminous works (Tokioka 1953, 1967). He revised and updated Oka's ascidian taxonomy on a great scale, followed, although still insufficiently, by me (Teruaki Nishikawa), working for Nagoya University (1979–2009) and Toho University (2009–2015). Further, marked contributions are memorable to ascidian taxonomy, including establishment of many new species, by many Japanese embryologists since the 1970s. Among them, Profs. Hiroshi Watanabe and

Yasunori Saito of the Shimoda Marine Research Center, University of Tsukuba and their collaborators have had an important role in the taxonomy of the family Botryllidae and several colonial genera of the family Styelidae through intimate life-history observations and/or histocompatibility experiments on cultured colonies (see Atsumi and Saito 2011 as the latest one). Watanabe was a student of Hidemichi Oka, a son of Asajiro Oka, showing another genealogy of Japanese ascidian taxonomy back to Oka.

26.3 Revision of Hartmeyer's 1906 Monograph of Japanese Ascidians

Table 26.1 shows a taxonomic revision of Hartmeyer's (1906) paper, one of the basic articles in the literature for Japanese ascidian taxonomy and nomenclature, based on my own reexamination of his specimens.

During my preparation for the revisions of the genera *Ciona* (Hoshino and Nishikawa 1985) and *Herdmania* (Nishikawa 2002a), and the Sea of Japan ascidians (Nishikawa 1990, 1991, 1992), etc., I had many chances to examine name-bearing type or other specimens deposited at natural history museums in Europe, the United States, and Australia and kindly sent to me by the courtesy of the museum curators concerned, together with the Oka and Tokioka collections in Japan. At that time, it was not very easy for Japanese taxonomists to visit foreign museums. It was fortunate, however, that since 1997 I have had several chances to visit some European museums to examine their ascidian collections as a whole, supported financially by JSPS (see Nishikawa 1999b; Mawatari 2003) and the Nagoya University Foundation (see Nishikawa and Sattmann 2001). Whenever I examined specimens there, I entertained a profound respect with sincere thanks to those who had kept the specimens in good condition for a very long time even during the World Wars. Their laborious efforts cannot be emphasized too repeatedly. I wish similar great respect would be deserved by Japanese museums.

Then, I noticed frequent occurrences of specimen exchanges, even name-bearing type specimens, among museums in Hartmeyer's days, without any published records remaining. In this sense, to visit various museums for comprehensive examination of the specimens concerned must be very fruitful for advancement in taxonomy and nomenclature. Such unnoticed exchanges of specimens will make some corrections to previous work inevitable, as illustrated by the case of *Styela elsa* Hartmeyer, 1906, shown next.

This species was established for two specimens, one from Okinose, Sagami Bay, 300 fathoms (~550 m) deep, and the other from Tanagawa, Osaka Bay, about 30 m (see Table 26.1). In Nishikawa's (1991) revision of this species, only the latter (ZMB2231) was available at the Museum für Naturkunde in Berlin, labeled as "Type!". The ZMB2231 specimen from Osaka Bay was much damaged and only 15 mm in the largest diameter, far smaller than the original description of the body size as 25 mm long, 33 mm high, and 21 mm wide. Therefore, Nishikawa (1991:101) regarded ZMB2231 as the paratype, with the then-missing "25 mm long" specimen as the holotype. Then, in the assumed conspecificity of these two specimens, *S. elsa* was synonymized with *Cnemidocarpa clara* (Hartmeyer, 1906), similar in morphology to the mentioned paratype.

This nomenclatural act should be corrected here under the International Code of Zoological Nomenclature, 4th edition (International Commission on Zoological Nomenclature 2000). Following Art 73.1, the mentioned two specimens of *S. elsa* are now regarded as its syntypes. In 1998, the other syntype specimen of *S. elsa* from Okinose, 35 mm in the largest diameter, was discovered in good condition at the Zoologische Staatssammlung München, registered ZSM924 and labeled as "Typus"; this specimen was identifiable with *C. fertilis fertilis* (Hartmeyer, 1906). Here, ZSM924 is designated as the lectotype, whereas ZMB2231 as the paralectotype, of *S. elsa*. Thus, *S. elsa* and *C. fertilis* are in synonymy, with the latter's priority over the former determined by the Principle of the First Reviser. *Styela elsa* should be excluded from the previous synonymy of *C. clara* given by Nishikawa (1991).

26.4 '*Halocynthia roretzi*' and '*H. hilgendorfi*' Revisited

As already stated, the Japanese ascidian fauna still awaits taxonomic revision using molecular and morphological information. The two species complexes of the genus *Halocynthia* are here mentioned for examples.

26.4.1 Halocynthia roretzi *Complex*

Halocynthia roretzi was established for a single ascidian collected from Japan (detailed locality not recorded) by Albrecht von Roretz during his stay in Japan from 1874 to 1882 as a medical doctor and later a professor at the medical colleges in Yokohama, Nagoya, Kanazawa, and Yamagata. As shown typically by Sawada et al. (2001) and Satoh (2014), this species has been used very frequently in Japan for morphological, embryological (including Evo-Devo), or pharmaceutical research; its frequent occurrences in nature and its aquaculture in Tohoku District have greatly helped such scientific studies by means of the stable material supply. Further, as previously mentioned, the familiar relationship of the Japanese people with this ascidian, lasting for more than 1000 years, also seems to have contributed to such remarkable ascidiological progress in Japan. The draft genome of *H. roretzi*, derived from an individual of 'Noon type' (see below) collected in Onagawa Bay (Sanriku District) and cultured in Mutsu Bay has been completely decoded (Prof. Hiroki Nishida of Osaka University, personal communication). The specific name "*roretzi*" was spelled originally as "*roretzii*" (see following), and the former should be regarded as an unjustified emendation. However, as "*H. roretzi* (von Drasche, 1884)" is doubtlessly in prevailing usage and attributed to the original author and date, it is here maintained as a justified emendation following Article 33.2.3.1 of the International Code of Zoological Nomenclature, 4th edition (International Commission on Zoological Nomenclature 2000).

Following Nishikawa's summary (1999a, thereby cited papers omitted; also see Satoh and Numakunai 1998), in the natural field of Mutsu Bay, northern end of Honshu, Japan, Drs. Takaharu Numakunai of Tohoku University and Zen'ichiro Hoshino of Iwate University discovered in the 1970s the often sympatric occurrence of the three types of ascidians attributable altogether to *Halocynthia roretzi*, defined by the remarkable differences in breeding season and spawning time; the Morning type breeds from the end of October to the middle of November and spawns in the evening with an optimal temperature of 16 °C, the Night type from early November to early December, spawning in the morning at 15 °C, and the Noon type from the middle of December to January, spawning around noon at 10 °C. It seems that they are reproductively isolated from one another in the field, although artificial fertilization of gametes from different types can result in 'hybrid' juveniles. Further, the three types are usually distinguishable from one another by the differences in external appearance, such as the tunic coloration, and the shape and density of mammillary projections over the body surface; so far as I am convinced, there are no detectable differences in internal morphology. Ascidians of each type begin to spawn at a specific latency after sunrise (or the artificial dark to light signal): the Morning, Noon, and Night types will begin to spawn 3.5 h, 6 h, and 10 h after sunrise, respectively. Each type may probably have its specific 'clock' to account for its own spawning time. Among the local populations whose spawning season and time was confirmed by Dr. Numakunai, the Noon type has been recorded from the Seto Inland Sea, the Sea of Japan coast of all Honshu to middle Hokkaido, Mutsu Bay, the Sanriku District (on Pacific Coast) and Ise Bay (on Pacific Coast), and probably also from Korean coasts, the Morning type from the Sea of Japan coast of all Hokkaido and rarely of the Shimokita Peninsula, and Mutsu Bay, whereas the Night type is from Mutsu Bay, its adjacent part of the Tsugaru Strait, and the Sea of Japan coast of middle Hokkaido; other previously recorded populations of *H. roretzi*, including the Vladivostok one, remain undetermined as to their 'type' identities.Please explain term 'do.' at first use.Dr. Sriuma kindly shows me that this problem is now under consideration by your language team.

Preliminary molecular analyses using some mitochondrial genes have so far failed to detect any significant differences among the types, which might possibly be caused by speciation too recent, say, toward the last (Würm) glacial period, to detect by previous methods. Further molecular studies are expected to elucidate the speciation processes in this species complex.

The holotype of *H. roretzi* deposited at the Naturhistorisches Museum Wien as Mollusca IN 101017 is very similar in external appearance to the figure of the original description (Drasche 1884), quite reminiscent of the Noon appearance. The museum label reads "*Cynthia Roretzii* v. Drasche Japan 1876 v. Roretz"; and this

"1876" may have indicated the therein deposited date in those days. Therefore, it follows that the specimen was collected before (or in) 1876. Until 1876, it is likely, on the basis of his biography, that he had only taken a 4-month trip in 1875 around the western part of Japanese Islands, where the Noon type has been exclusively recorded (see foregoing). Thus, the binomen may safely be attributable to the Noon type, although its strict definition (using spawning season and time) is inapplicable to the dead holotype. Further nomenclatural considerations should be made when the species status of each type is elucidated.

26.4.2 **Halocynthia hilgendorfi** *Complex*

The species of the genus *Halocynthia* with spiny side-branched tunic processes and a branched (never round nor massive) gonad on each side was once treated altogether as *Halocynthia hispida* (Herdman, 1881) by Nishikawa (1991:145–147), followed by Nishikawa (1995). Later, Nishikawa (1999a) denied this, claiming that 'the *Halocynthia*' thus defined may contain two species, *H. hilgendorfi* (Traustedt, 1885) and *H. ritteri* Oka, 1906, with preliminary limited usage of *H. hispida* only to the Australian population.

The reason was, according to Nishikawa's summary (1999a: thereby cited papers omitted here; also see Satoh and Numakunai 1998), that the mitogenomic restriction fragment-length polymorphism (RFLP) analyses by Dr. Tsuneo Kakuda revealed the existence of two distinct groups in 'the *Halocynthia*' defined here; they differed from each other also in external morphology, one furnished with the long-stem spiny processes confined to both apertures and vicinities, and the other with the processes not confined to siphons, but also discernible densely or sparsely elsewhere; some other morphological differences were also detected between the two. The former can be referred to as *H. ritteri* Oka, 1906, and the latter as *H. hilgendorfi* (probably with *H. igaboja* Oka, 1906 and *H. owstoni* Oka, 1906 as junior synonyms), on the basis of original descriptions and my reexamination of the syntypes of *H. hilgendorfi* (see Table 26.1). Further global molecular and morphological analyses are expected including the two Japanese species, *H. hispida* sensu stricto around Australia [now called *H. dumosa* (Stimpson, 1855), see Kott (1998)], and *H. okai* Ritter, 1907 on the Pacific Coast of North America, and allies; special attention should be paid to *H. dumosa* where the distribution of long-stem spiny processes was variable ranging from the mentioned "*ritteri*" to "*hilgendorfi*" patterns (Kott 1985:342–343).

Table 26.2 Comparison of photosymbiotic species of the genus *Diplosoma* known from Japanese waters, with mentioned data only from Japanese specimens

Species	Stigma pattern	Type in retractor muscle issuing	Larval trunk length (mm)	Number of larval adhesive papillae	Number of larval ampullae	References
D. ooru	5654	T	0.5	3	2 pairs	Oka et al. (2005)
D. simileguwa	4543	T				Oka et al. (2005)
D. simile	6665	T		3		Hirose and Oka (2008)
D. variostigmatum	Variable	T	~0.6[a]	3	4 pairs	Hirose and Oka (2008)
D. watanabei	6765 or 6764	T	~0.6[a]	3	2 pairs	Hirose et al. (2009a)
D. virens	6665	N				Hirose and Oka (2008)
D. aggregatum	6665	N	~0.8[a]	3	3 pairs	Hirose and Hirose (2009)
D. gumavirens	5554	N	~0.3[a]	12–16	3 pairs	Hirose et al. (2009b)

For further details, see the text

[a] Roughly measured from figures

26.5 Recent Advances in Didemnid Taxonomy

The family Didemnidae is a group of colonial ascidians ‘notorious’ for its difficulties in taxonomy and identification, because of its easy-to-shrink small zooids (often only 1 mm or less) with simpler structure and of the generic and specific classifications based largely on detailed features of gonads detectable only in fully matured specimens and well-preserved conditions. Fortunately, the molecular phylogenetic analyses by Yokobori et al. (2006) using the nuclear 18S rRNA gene indicated a monophyletic origin of this family and also the reciprocal monophyly of the two genera *Didemnum* and *Diplosoma* defined morphologically in a prevailing traditional system. Morphology may probably make sense to didemnid taxonomy at the genus level. At the species level, it has been long disputed what kinds of morphological characters are reliable and useful for species delimitation only on unstable grounds usually lacking any good objective evidences. However, recent molecular and morphological analyses have begun to clearly solve this problem, as exemplified by Prof. Hirose and his collaborators’ taxonomic studies on photosymbiotic didemnids.

26.5.1 *Taxonomy of Photosymbiotic Species of* Diplosoma

Until the taxonomic studies by Prof. Hirose et al. on photosymbiotic species of the genus *Diplosoma*, only a single such species, *D. midori* (Tokioka, 1954), had been known from Japanese waters, recorded solely from the Tokara Islands, northern Ryukyus; this species has been often synonymized with D. *simile* (Sluiter, 1909). Now, as shown in Table 26.2, the following eight species are known from the Ryukyus: *D. simile*, *D. virens* (Hartmeyer, 1909), *D. ooru* Hirose and Suetsugu in Oka et al. (2005), *D. simileguwa* Oka and Hirose in Oka et al. (2005), *D. variostigmatum* Hirose and Oka, 2008, *D. watanabei* Hirose and Oka in Hirose et al. (2009a), *D. gumavirens* Hirose and Oka in Hirose et al. (2009b), and *D. aggregatum* Hirose and Hirose, 2009. *Diplosoma midori* is treated as a species of uncertain identity by Oka et al. (2005).

These species are markedly distinguishable from one another by using partial sequences of the mitochondrial COI gene (and in some cases also by the nuclear 18S rRNA gene). Interestingly, Prof. Hirose and collaborators have proven that each species thus delimited has a unique stigma pattern, except for *D. variostigmatum* (see Table 26.2). The stigma pattern is represented by the number of stigmata in each half row from the first (anteriormost) to the fourth (posteriormost) rows; for example, a “4543” pattern means four stigmata in the first row, five in the second, four in the third, and three in the fourth. The pattern in each species is almost always invariable among zooids of a colony, or different colonies at a locality, and even colonies from different localities, so far as their surveys have confirmed, and therefore, is a good key character for discriminating one species from another. Further, there are two types in the issuing mode of retractor muscle from the zooid; in the T-type the muscle issues from the bottom of the thorax whereas it issues from the esophageal neck in the N-type. Each species has been proved to always have one of those types. Molecular phylogenetic analyses have shown, using partial sequences of the COI gene, that all the analyzed photosymbiotic species of *Diplosoma* constitute a monophyletic group, and are divided into two distinct clusters, one with the species with the T-type retractors, and the other with the N-type. In this way, their morphological and molecular studies have given fruitful results. Further analyses are expected for widely sampled materials, including the type localities of *D. virens* (Ceylon; as *Diplosoma viride* Herdman, 1906, replaced by a new name, *D. virens*) and *D. simile* (Celebes and Aru Islands).

26.5.2 *Morphological Differences Revealed as a Sign of Speciation in the* Didemnum molle *Complex*

Vase-shaped ascidian colonies harboring photosymbiotic unicellular algae inside are very common in lagoons and surroundings in the Indo-West Pacific, including the Ryukyus, and identified with *Didemnum molle* (Herdman, 1886). They are called in Japanese 'chatsubo-boya,' with 'chatsubo' meaning a pot to store tea leaves. This species has been regarded as greatly variable in colony size and surface coloration, but the molecular analyses by Hirose et al. (2009a), using partial sequences of the COI gene, have revealed that such morphological differences are attributable to the result of speciation.

In the Ryukyus, four morphotypes are recognized: three color morphs (white, dark gray, and brown) of small-sized colonies, and a large-sized white morph with gray patches. The tree topology of Hirose et al. (2009b) clearly indicated that the four morphs constitute a monophyletic group, distinct from other analyzed didemnids, and divided into four clades corresponding to each morph. Therefore, they concluded that the four morphs may probably represent "discrete sibling species." They failed to find any morphological characters other than the mentioned colony coloration and size to distinguish one form from another among the four (Hirose et al. 2010; Nagaya and Hirose 2013). Their nomenclatural conclusion remains unsettled, and further considerations are highly expected. Anyway, this discovery of sibling species has doubtlessly given a new perspective to comparative studies in the *D. molle* complex, as initiated by Hirabayashi et al. (2006).

26.6 Notes on Alien Ascidians in Japan

26.6.1 East Asia as a Source of Alien Ascidians

Many Japanese or East Asian ascidians may have had chances to move artificially to other regions. Among such ascidians, *Styela clava* Herdman, 1881 has become one of the world-notorious invaders. Its alien occurrence was first recognized by Tokioka (1955) in England, where *S. mammiculata* Carlisle, 1954 was established for the specimens collected in 1953 from a buoy or oyster bed, and later synonymized with *S. clava* by Tokioka (1955) and Millar (1960). Even by using various molecular markers, pathways of the spread of this species remain obscure (Dupont et al. 2010; Goldstein et al. 2011).

Another notoriously invasive ascidian, *Didemnum vexillum* Kott, 2002, was inferred to be of Far Eastern (probably Japanese) origin by Lambert (2009), mainly because its oldest known colonies were collected in 1926 from Mutsu Bay, northern Japan (Nishikawa 1990). Recently, another colony was found in the University Museum, University of Tokyo, as UMUTZ Tu-43, collected from outside Yokohama Port in April 1923 (Nishikawa, accepted), 3 years before the first occurrence in Mutsu Bay. The new collection year may reinforce the hypothesis of a Far Eastern or Japanese origin of this species, but in contrast, the locality of "outside of Yokohama Port" might suggest the possibility that even the Japanese population is nonindigenous. It is true that *D. vexillum* inhabits either natural or artificial substrata on Japanese coasts. However, to live on the natural substrata does not always indicate that the organism is indigenous. The bivalve *Mytillus galloprovincialis* Lamarck, 1819, obviously of European origin, is often found on intertidal or subtidal rocky shores in middle Japan (Nishikawa, personal observation). Recent global molecular analyses of *D. vexillum* colonies from Japan, New Zealand, NE Europe, and the East and West coasts of the USA, using partial sequences of the mitochondrial COI and the nuclear THO2 genes, by Stefaniak et al. (2012) found an extremely large number of unique haplotypes only in Japanese populations, and therefore concluded that Japan lies within the native range of this species.

26.6.2 Alien Ascidians in Japan

At present the following seven species seem obviously nonindigenous ascidians introduced to Japan and now flourishing there, to list in the order of discovery: *Molgula manhattensis* (De Kay, 1843) since 1972 (see Nishikawa 2002d); *Polyandrocarpa zorritensis* (Van Name, 1931) since 1991 (see Nishikawa 2002e); *Phallusia philippinensis* Millar, 1975 in the sense of Vandepas et al. (2015) since 1999 or earlier (see below); *Microcosmus squamiger* Michaelsen, 1927 since 2007 (see below); *Ascidiella aspersa* (Müller, 1776) since 2008 (see Nishikawa et al. 2014); the Atlantic form of *Clavelina lepadiformis* (Müller, 1776) complex since 2011 (see following); and *Microcosmus exasperatus* Heller, 1878 since 2014 (see following). The *Ciona intestinalis* (Linnaeus, 1767) complex and *Styela plicata* (Lesueur, 1823), whose Japanese populations have been often thought nonindigenous because of their successful colonization on artificial structures, are treated here as cryptogenic species (for details, see Nishikawa 2012).

26.6.2.1 *Phallusia philippinensis*

According to the molecular and morphological analyses by Vandepas et al. (2015) of *Phallusia nigra* Savigy, 1816 and allies, *P. philippinensis* in their sense, as distinct from *P. nigra* Savigy, 1816, was first discovered from a marina of Okinawa Island, probably around 1999, by Hirose (1999, as *P. nigra*), and in 2014 found abundantly from some marinas there (Nagayama, unpublished). The Okinawan population was regarded nonindigenous by Vandepas et al. (2015: 60).

26.6.2.2 *Microcosmus squamiger*

Nishikawa and Ueda (2011) reported finding *M. squamiger* since 2007 at eight sites on the Pacific Coast of the Boso Peninsula, Tokyo Bay, Sagami Bay, and the Seto Inland Sea; at two of the eight sites, no more specimens were detected in 2010 or 2011. Since 2012, this species has also been collected from some fishery ports in

Suruga Bay and from Kushimoto, southern tip of the Kii Peninsula (Nishikawa, unpublished), other than some new sites in Sagami Bay. Further in 2014, the species was collected from a fishery port of Okinawa Island (Nagayama, unpublished). In Japanese waters, this species seems to mature in summer, as do the introduced Mediterranean populations (Rius et al. 2009). Its economic damages have not yet been reported in Japan, but its firm attachment to fishery nets and ropes may be a potential danger to fisheries, if swarming densely. Therefore, continuous monitoring of this alien species must be necessary over all the Japanese coasts.

26.6.2.3 Atlantic Form of *Clavelina lepadiformis* Complex

Nishikawa et al. (2013) detected by morphological and molecular analyses the first occurrence in 2011 of the Turon et al. (2003) Atlantic form of an European social ascidian, *Clavelina lepadiformis* complex, from the Japanese waters (outside a fishery port in Suruga Bay, 28 m deep); the other, Mediterranean form of the complex has not yet been discovered in Japan. The Atlantic form has so far been known from many fishery ports only along Suruga Bay.

In the enclosed Nishina-hama Fishery Port, Shizuoka Prefecture, monthly sampling was carried out from February 2013 to September 2014. The breeding season may be supposed from November to May with water temperatures of 14–20 °C, as judged from the occurrence of zooids with embryos brooded in the thorax. The density was highest in April and May, decreased rapidly in June, going down to zero in August and September, and again recovered in winter (Nishikawa et al., in preparation). The population dynamics in Nishina-hama may be similar to that of the Mediterranean (interior) populations of the Atlantic form analyzed by Caralt et al. (2002).

26.6.2.4 *Microcosmus exasperatus*

This species was found for the first time from Japanese waters in 2014 at several marinas and fishery ports in Okinawa Island (Nagayama, unpublished). It has been rightly distinguishable from the congeners with an elongated gonad composed of two or three lobes on each side by the sharply pointed and widely based siphonal spinules, as confirmed for the syntypes collected from Jamaica and registered in the Naturhistorisches Museum Wien as Mollusca IN 100829 (Nishikawa, unpublished). This species "appears to be pan-tropic" (Kott 1985:348), probably because of human-mediated migration, but the possibility of cryptic speciation cannot be also denied. Future global phylogeographic analyses are greatly anticipated.

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References

Atsumi MO, Saito Y (2011) Studies on Japanese botryllid ascidians. V. A new species of the genus *Botrylloides* very similar to *Botrylloides simodensis* in morphology. Zool Sci 28:532–542

Caralt S, López-Legentil S, Tarjuelo I, Uriz MJ, Turon X (2002) Contrasting biological traits of *Clavelina lepadiformis* (Ascidiacea) populations from inside and outside harbours in the western Mediterranean. Mar Ecol Prog Ser 244:125–137

Dupont L, Viard F, Davis MH, Nishikawa T, Bishop JDD (2010) Pathways of spread of the introduced ascidian *Styela clava* (Tunicata) in Northern Europe, as revealed by microsatellite markers. Biol Invasions 12:2707–2721

Goldstein SJ, Dupont L, Viard F, Hallas PJ, Nishikawa T, Schiel DR, Gemmell NJ, Bishop JDD (2011) Global phylogeography of the widely introduced North West Pacific ascidian *Styela clava*. PLoS One 6:e16755

Harada E (1991) Inventory of zoological type specimens in the Museum of the Seto Marine Biological Laboratory. Publ Seto Mar Biol Lab 35:171–233

Hartmeyer R (1906) Ein Beitrag zur Kenntnis der japonischen Ascidienfauna. Zool Anz 31:1–30

Herdman WA (1882) Report on the Tunicata collected during the voyage of H.M.S. *Challenger* during the years 1873–1876. Pt I. Ascidiae simplices. Rep Challenger Exp 6:1–296

Herdman WA (1886) Report on the Tunicata collected during the voyage of H.M.S. *Challenger* during the years 1873–1876. Pt II. Ascidiae compositae. Rep Challenger Exp 14:1–399

Hirabayashi S, Kasai F, Watanabe MM, Hirose E (2006) Contents of ultraviolet-absorbing substances in two color morphs of the photosymbiotic ascidian *Didemnum molle*. Hydrobiologia 571:419–422

Hirose E (1999) Pigmentation and acid storage in the tunic: protective functions of the tunic cells in the tropical ascidian *Phallusia nigra*. Invertebr Biol 118:414–422

Hirose M, Hirose E (2009) DNA barcoding in photosymbiotic species of *Diplosoma* (Ascidiacea: Didemnidae), with the description of a new species from the southern Ryukyus, Japan. Zool Sci 26:564–568

Hirose E, Oka AT (2008) A new species of photosymbiotic ascidian from the Ryukyu Archipelago, Japan, with remarks on the stability of stigma number in photosymbiotic *Diplosoma* species. Zool Sci 25:1261–1267

Hirose E, Oka AT, Hirose M (2009a) Two new species of photosymbiotic ascidians of the genus *Diplosoma* from the Ryukyu Archipelago, with partial sequences of the COI gene. Zool Sci 26:362–368

Hirose M, Yokobori S, Hirose E (2009b) Potential speciation of morphotypes in the photosymbiotic ascidian *Didemnum molle* in the Ryukyu Archipelago, Japan. Coral Reefs 28:119–126

Hirose M, Tochikubo T, Hirose E (2010) Taxonomic significance of tunic spicules in photosymbiotic ascidians: a quantitative and molecular evaluation. J Mar Biol Assoc U K 90:1065–1071

Hoshino Z, Nishikawa T (1985) Taxonomic studies of *Ciona intestinalis* (L.) and its allies. Publ Seto Mar Biol Lab 30:61–79

International Commission on Zoological Nomenclature (2000) International code of zoological nomenclature, 4th edn (in Japanese). Union of Japanese Societies for Systematic Zoology, Sapporo

Kott P (1985) The Australian Ascidiacea: part I. Mem Qd Mus 23:1–440

Kott P (1998) Tunicata. In: Wells A, Houston WWK (eds) Zoological catalogue of Australia, vol 34. CSIRO, Australia, pp 51–252

Kurabayashi A, Okuyama M, Ogawa M, Takeuchi A, Jing Z, Naganuma T, Saito Y (2003) Phylogenetic position of a deep-sea ascidian, *Megalodicopia hians*, inferred from the molecular data. Zool Sci 20:1243–1247

Lambert G (2009) Adventures of a sea squirt sleuth: unraveling the identity of *Didemnum vexillum*, a global ascidian invader. Aquat Invasions 4:5–28

Mawatari SF (2003) Taxonomic studies on Prof. Ludwig Döderlein's collection of Japanese animals. Hokkaido University, Sapporo

Millar RH (1960) The identity of the ascidians *Styela mammiculata* Carlisle and *S. clava* Herdman. J Mar Biol Assoc UK 39:509–511

Monniot C, Monniot F, Gaill F (1975) Les Sorberacea: une nouvelle classe de tuniciers. Arch Zool Exp Gén 116:77–122

Nagaya K, Hirose E (2013) Pattern of stigma numbers as a taxonomic character in some didemnid ascidians (Aplousobranchia: Didemnidae). Zootaxa 3608:87–93

Nara National Research Institute for Cultural Properties (2015) The wooden tablet image database, http://jiten-en.nabunken.go.jp/index.html and http://www.nabunken.go.jp/Open/mokkan/mokkan.html. Accessed 14 Dec 2015

Nishikawa T (1980) Contributions to the Japanese ascidian fauna XXXII. Taxonomic review of the species group of *Pyura sacciformis* (von Drasche, 1884). Publ Seto Mar Biol Lab 25:79–93

Nishikawa T (1981) Contributions to the Japanese ascidian fauna. XXXIV. Record of *Bathypera ovoida* (Ritter, 1907) from Sagami Bay. Publ Seto Mar Biol Lab 26:187–190

Nishikawa T (1986) Some ascidians dredged around the Oki Islands, the Japan Sea. Mem Natl Sci Mus Tokyo 19:175–184

Nishikawa T (1990) The ascidians of the Japan Sea. I. Publ Seto Mar Biol Lab 34:73–148

Nishikawa T (1991) The ascidians of the Japan Sea. II. Publ Seto Mar Biol Lab 35:25–170

Nishikawa T (1992) The ascidians of the Japan Sea. III. Publ Seto Mar Biol Lab 35:303–334

Nishikawa T (1995) Subphylum Urochordata. In: Nishimura S (ed) Guide to seashore animals of Japan with color pictures and keys, vol 2. Hoiku-sha, Osaka, pp 573–608

Nishikawa T (1999a) Sibling species of ascidians and their modes of speciation. In: Okutani T, Ohta S, Ueshima R (eds) Updated progress in aquatic invertebrate zoology. Tokai University Press, Tokyo, pp 309–324

Nishikawa T (ed) (1999b) Preliminary taxonomic and historical studies on Prof. Ludwig Döderlein's collection of Japanese animals made in 1880–81 and deposited at several European museums. Nagoya University, Nagoya

Nishikawa T (2000) Protochordata. In: Aoki J, Tajika K, Morioka H (eds) Systematic zoology (supplement). Nakayama-shoten, Tokyo, pp 334–343

Nishikawa T (2002a) Revision of the ascidian genus *Herdmania* (Urochordata: Ascidiacea) inhabiting Japanese waters. Species Divers 7:217–250

Nishikawa T (2002b) Dr. Takasi Tokioka (1913–2001). Plankton Biol Ecol 49:47

Nishikawa T (2002c) To the memory of Dr. Takasi Tokioka (1913–2001). Nankiseibutu 44:1–3

Nishikawa T (2002d) *Molgula manhattensis*. In: The Ecological Society of Japan (ed) Handbook of alien species in Japan. Chijin-shokan, Tokyo, p 178

Nishikawa T (2002e) *Polyandrocarpa zorritensis*. In: The Ecological Society of Japan (ed) Handbook of alien species in Japan. Chijin-shokan, Tokyo, p 179

Nishikawa T (2006) Second record of *Pyura comma* (Hartmeyer, 1906) from Sagami Bay and adjacent waters, Japan (Urochordata: Ascidiacea). Mem Natl Sci Mus Tokyo 41:329–334

Nishikawa T (2012) Recent topics on the biology of alien ascidians. Sessile Organisms 29:61–68

Nishikawa T (accepted) Ascidians deposited in the Department of Zoology, the University Museum, the University of Tokyo. In: Ueshima R (ed) Catalogue of invertebrate collection deposited in the Department of Zoology, the University Museum, the University of Tokyo, Part 3

Nishikawa T, Otani M (2004) Occurrence of the European ascidian *Ascidiella scabra* (Müller, 1776) in the 19th century in Nagasaki, Japan, probably as an ephemeral alien species. Contrib Biol Lab Kyoto Univ 29:401–408

Nishikawa T, Sattmann H (2001) List of Dr. Albrecht von Roretz's collection of Japanese animals made about 120 years ago, compiled from the catalogues of Naturhistorisches Museum Wien. Bull Nagoya Univ Mus 17:33–44

Nishikawa T, Ueda I (2011) Dynamics of an alien ascidian, *Microcosmus squamiger* Michaelsen, 1927 in the Japanese waters. Paper presented at the 47th annual meeting of the Japanese Society for Systematic Zoology, University of the Ryuyus, 4–5 June 2011

Nishikawa T, Ikezaki S, Kuriiwa K, Kubota S (2013) Occurrence of Atlantic form of *Clavelina lepadiformis* complex in Japan. Paper presented at the 84th Annual Meeting of the Zoological Society of Japan, Okayama University, 26–28 September 2013

Nishikawa T, Oohara I, Saitoh K, Shigenobu Y, Hasegawa N, Kanamori M, Baba K, Turon X, Bishop JDD (2014) Molecular and morphological discrimination between an invasive ascidian, *Ascidiella aspersa*, and its congener *A. scabra* (Urochordata: Ascidiacea). Zool Sci 31:180–185

Oka A (1892) Die periodische Regeneration der oberen Körperhäfte bei den Diplosomiden. Biol Centbl 12:265–268

Oka A (1906) Notizen über japanische Ascidien I. Annot Zool Jpn 6:37–52

Oka A (1914) Notizen über japanische Ascidien. II. Annot Zool Jpn 8:443–458

Oka A (1935a) Report of the biological survey of Mutsu Bay. 28. Ascidiae simplices. Sci Rep Tohoku Imp Univ 10:427–466

Oka A (1935b) Überblick über die japanische Ascidienfauna. Proc Imp Acad 11:198–200

Oka A, Willey A (1892) On a new genus of synascidians from Japan. Q J Microsc Sci NS 33:313–324

Oka AT, Suetsugu M, Hirose E (2005) Two new species of *Diplosoma* (Ascidiacea: Didemnidae) bearing prokaryotic algae *Prochloron* from Okinawajima (Ryukyu Archipelago, Japan). Zool Sci 22:367–374

Rius M, Pineda MC, Turon X (2009) Population dynamics and life cycle of the introduced ascidian *Microcosmus squamiger* in the Mediterranean Sea. Biol Invasions 11:2181–2194

Satoh N (2014) Developmental genomics of ascidians. Wiley, Hoboken

Satoh N, Numakunai T (1998) Approaches to speciation. In: Satoh N (ed) Biology of ascidians. University of Tokyo Press, Tokyo, pp 121–131

Satoh N, Rokhsar D, Nishikawa T (2014) Chordata evolution and the three-phylum system. Proc R Soc B 281:20141729

Sawada H, Yokosawa H, Lambert CC (eds) (2001) The biology of ascidians. Springer, Tokyo

Shenkar N, Swalla BJ (2011) Global diversity of Ascidiacea. PLoS One 6(6):e20657

Sterfaniak L, Zhang H, Gittenberger A, Smith K, Holsinger K, Lin SJ, Whitlatch RB (2012) Determining the native region of the putatively invasive ascidian *Didemnum vexillum* Kott, 2002. J Exp Mar Biol Ecol 422–423:64–71

Tatián M, Lagger C, Demarchi M, Mattoni C (2011) Molecular phylogeny endorses the relationship between carnivorous and filter-feeding tunicates (Tunicata, Ascidiacea). Zool Scr 40:603–612

Tokioka T (1953) Ascidians of Sagami Bay. Iwanami-shoten, Tokyo

Tokioka T (1954) Contributions to the Japanese ascidian fauna. IX. Re-description of Oka's species found in "Figuraro de Japanaj Restoj". Publ Seto Mar Biol Lab 4:69–74

Tokioka T (1955) Record of *Styela clava* Herdman from the European waters. Dobutsugaku Zasshi (Zool Mag Jpn) 64:200

Tokioka T (1963) Contributions to the Japanese ascidian fauna. XX. The outline of Japanese ascidian fauna as compared with that of the Pacific coasts of North America. Publ Seto Mar Biol Lab 11:131–156

Tokioka T (1967) Pacific Tunicata of the United States National Museum. US Natl Mus Bull 251:1–247

Traustedt M (1885) Ascidiae simplices fra det stille Ocean. Vidensk Medd Dan Nathist Foren 1884:1–60

Traustedt M, Weltner W (1894) Bericht über die Herrn Dr. Sander gesammelten Tunicaten. Arch Naturgesch 60:10–14

Tsagkogeogra G, Turon X, Hopcroft R, Tilak M, Feldstein T, Shenkar N, Loya Y, Huchon D, Douzery EJP, Delsuc F (2009) An updated 18S rRNA phylogeny of tunicates based on mixture and secondary structure models. BMC Evol Biol 9:187

Turon X, Tarjuelo I, Duran S, Pascual M (2003) Characterising invasion processes with genetic data: an Atlantic clade of *Clavelina lepadiformis* (Ascidiacea) introduced into Mediterranean harbours. Hydrobiologia 503:29–35

Vandepas LE, Oliveira LM, Lee SSC, Hirose E, Rocha RM, Swalla BJ (2015) Biogeography of *Phallusia nigra*: is it really black and white? Biol Bull 228:52–64

von Drasche R (1884) Über einige neue und weniger bekannte ausser-europäische einfache Ascidien. Denkschr Akad Wiss Wien 48:369–386

Wada H (1998) Evolutionary history of free-swimming and sessile life styles in urochordates as deduced from 18S rDNA molecular phylogeny. Mol Biol Evol 15:1180–1194

Yamaguchi T (ed) (1987) Von Siebold and natural history of Japan. I: Studies on the unpublished specimens of Japanese animals collected by von Siebold and still preserved in the museums of the Netherlands. Kumamoto University, Kumamoto

Yokobori S, Kurabayashi A, Neilan BA, Maruyama T, Hirose E (2006) Multiple origins of the ascidian–*Prochloron* symbiosis: molecular phylogeny of photosymbiotic and non-symbiotic colonial ascidians inferred from 18S rDNA sequences. Mol Phylogenet Evol 40:8–19

Chapter 27
A Taxonomic Review of Lancelets (Cephalochordata) in Japanese Waters

Teruaki Nishikawa

Abstract Until the 1980s, the Japanese lancelet fauna had been believed to contain a single species, but now the number of species becomes six in total, covering all the three known genera: *Branchiostoma japonicum* (Willey, 1897); *Asymmetron lucayanum* Andrews, 1893 complex spp. A and B; *A. inferum* Nishikawa, 2004; *Epigonichthys maldivensis* (Cooper, 1903); and *E. cultellus* Peters, 1876. A brief history is traced and a taxonomic consideration is made for respective species.

Keywords Lancelets • Molecular phylogenetics • Morphology • *Branchistoma* • *Asymmetron* • *Epigonichthys* • Japan • China

27.1 Introduction

Lancelets are fish-like invertebrates, consisting of about 30 known species in two genera in an excellent monograph given by Poss and Boschung (1996). Later, a third genus was recovered from an invalid status by Nishikawa (2004), and this revised three-genus system has been supported by subsequent molecular phylogenetic analyses (Nohara et al. 2005; Kon et al. 2007; Li et al. 2014). Furthermore, several cryptic species have been detected as shown here. Adults live within the surface layer of bottom sand as filter-feeders in tropical and temperate shallow waters all over the world; their larvae are planktotrophic, having a long pelagic duration even offshore. Habitat depth ranges from intertidal (for most species) down to 229 m (for *Asymmetron inferum* Nishikawa, 2004, see Sect. 27.4). They have long been treated as the subphylum Cephalochordata in the phylum Chordata, but recently given a full phylum rank by Satoh et al. (2014).

Lancelets are called in Japan as ‘namekuji-uo’ (slug-fish), coined in the early Meiji period from the historical background that they were first positioned in the slug genus *Limax* by Pallas (1774). The material was probably supplied to him as

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dried specimen(s), with the ventral flat part remaining between the left and right metapleurae, which was then possibly misunderstood as a molluscan foot. The first usage of ‘namekuji-uo’ dates back to 1876, 6 years before the actual discoveries of lancelets in Japan in 1882 (for further details, see Nishikawa 1995a). The name was long applied also to the single species of the genus *Branchiostoma*, referring in the past to *B. belcheri* (Gray, 1847) but now to *B. japonicum* (Willey, 1897) (as shown in Sect. 27.2). Until the 1980s, the Japanese lancelet fauna had been believed to contain this species only, to which are now added are another five species: *Asymmetron lucayanum* Andrews, 1893 complex spp. A and B; *A. inferum* Nishikawa, 2004 (as the first deep-water species among lancelets); *Epigonichthys maldivensis* (Cooper, 1903); and *E. cultellus* Peters, 1876. Thus, it seems doubtless that the Japanese lancelet fauna has a very high diversity, covering all the valid three genera, almost comparable with the Hong Kong fauna composed of *B. belcheri*; *B. japonicum*; *B. malayanum* Webb, 1956; *A. lucayanum* species complex; and *E. cultellus* (see Chen et al. 2007). The Japanese population of *B. japonicum* is ranked as “Nearly Threatened” in Japanese Association of Benthology (2012), and such may hold almost true with other shallow-water lancelets in Japan. Our attention should be drawn to their preservation.

27.2 *Branchiostoma japonicum* (Japanese Name: higashi-namekuji-uo)

The Japanese population of the genus *Branchiostoma* had been called only ‘namekuji-uo,’ without any binomina, until Andrews (1895) identified the material from “Shikajima” (=Shikanoshima Islet in the Genkainada Sea, northern Kyushu) “provisionally” with *B. belcheri*. Later, Willey (1897, footnote in p. 220) validly established a new infraspecific taxon *Amphioxus belcheri* var. *japonicus* by a bibliographic reference to Andrews’ (1895) description; thus, the type locality of the binomen *Branchiostoma japonicum* is Shikanoshima Islet. Afterward, from the 1920s to the early 2000s, the Japanese population was predominantly (although never unanimously) called *B. belcheri*, as a senior synonym of *B. japonicum* (for further historical details, see Nishikawa 1981). Nishikawa (1981) first claimed that the Japanese population is similar to that of Kiaochow Bay, Qingdao, northern China, rather than that of Xiamen (=Amoy), southern China, in terms of some meristic characters, especially the number of preanal fin-chambers; the Kiaochow population was separated morphologically from the Xiamen one by Tchang and Koo (1936), giving the former a new name, *B. belcheri* var. *tsingtauense*.

In the early 2000s, an astonishing fact was revealed by Wang et al. (2004) and Xu et al. (2005), using mitochondrial DNA sequence information, that the Xiamen area is inhabited by two distinct *Branchiostoma* species, usually collected simultaneously (see Zhang et al. 2006); one of the two is very similar to Japanese specimens in the DNA database, which therefore Wang and Fang (2005) and Zhang et al. (2006) referred to as *B. japonicum* (with *B. tsingtauense* as its junior synonym, based on Nishikawa's (1981) claim), while naming the other as *B. belcheri* without enough evidence. Now the nomenclatural act concerning *B. japonicum* is validated by Zhong et al. (2009), including molecular information of Qingdao material, and by Xiao et al. (2008), using that from the Genkainada Sea (close to the type locality of *B. japonicum*, see earlier); this species localities other than Japan, Qingdao, and Xiamen have been confirmed using molecular marker (s) to be Weihai by Zhao and Zhu (2011) and Rizhao by Xiao et al. (2008) in northern China, and Hong Kong in southern China by Chen et al. (2007). On the other hand, the afore-stated nomenclatural act on *B. belcheri* by Wang and Fang (2005) and Zhang et al. (2006) is now supported by our molecular comparison of Chinese specimens with those from its type locality, Borneo (Kon et al., submitted). *Branchiostoma belcheri* thus defined has been recorded from Xiamen (Wang et al. 2004; Xu et al. 2005) and Maoming (Zhong et al. 2009; Li et al. 2013), in the South China Sea, and from Beihai, Gulf of Tonkin (=Beibu Gulf) (Li et al. 2013), as well as from Borneo (Gray 1847).

Our global molecular phylogenetic studies of *Branchiostoma* have revealed several cryptic species similar in morphology to *B. belcheri*/*B. japonicum* (Kon et al., submitted), but no such species has appeared in Chinese and Japanese waters. On these grounds, Table 27.1 shows a morphological comparison among local populations of *B. japonicum* and *B. belcheri*; the two are roughly distinguishable from each other by the different number of preanal fin-chambers (41–73 in the former, and 69–105 in the latter). They differ also in the diploid chromosome number, 36 in the Japanese (Saotome and Ojima 2001) and Xiamen (Zhang et al. 2009) populations of *B. japonicum*, and 40 in the Xiamen population of *B. belcheri* (Zhang et al. 2009).

Thus, it seems quite safe to say that the waters around Japan (excepting Hokkaido in the north and the Ryukyu Archipelago in the south; numerous reports on local occurrences and/or habitat information not shown) and along northern China are inhabited only by *B. japonicum*. Therefore, the materials collected from these areas and referred to previously as "*B. belcheri*" or "*B. belcheri tsingtauense*" in numerous papers and reports, may be safely read as *B. japonicum*, including the Japanese "*B. belchri*" specimen with its whole mitogenome sequence registered as AB078191 in the DDBJ/EMBL/GenBank (see the explanation for Fig. 27.2). The Japanese name for the Japanese population of *B. japonicum* should be 'higashi-namekuji-uo,' coined by Dr. Kinya Yasui in Yasui and Kubokawa (2005). On the other hand, many papers on "*B. belcheri*" in the Xiamen area published before the early 2000s may often have included information of *B. belcheri* and *B. japonicum* together, as exemplified by Chin's measurements (Chin 1941; table 5) of preanal fin chambers ranging from 35 to 90 for the Liuwutien (as the famous fishery ground there) specimens; these figures may have derived from both *B. japonicum* (with 48–64 chambers, see Table 27.1) and *B. belcheri* (with 80–103).

Table 27.1 shows a tendency in *B. japonicum* that northern populations from Japan to Qingdao have a few more myomeres than southern ones of Xiamen and Hong Kong; the Japanese (excluding the Ariake Sea) and North China specimens are provided with 63–69 myomeres, the Ariake Sea ones with 62–66, and the

Table 27.1 A morphological comparison among local populations of molecularly defined *Branchiostoma japonicum* and *B*. *belcheri*, with information about breeding season and larval duration

Species name	Locality	Number of Dorsal fin-chambers	Preanal fin-chambers	Total myomeres	Breeding season	Onset of spawning	Pelagic larval duration (days)	Notes and references
B. *japonicum*	Japan (except Ariake Sea)	260–350	47–68	63–69	July–Aug	2000–2200	55	Nishikawa (1981), Mizuta and Kubokawa (2004), and Ueda and Kamakura (2006)
	Ariake Sea	251–310	46–66	62–66	June–July			Hemni and Yamaguchi (2003a, b)
	Changli, Sea of Bohai	276–340	47–66	65–68				Yan et al. (2005)
	Weihai, E of Qingdao	269–339	41–69	65–69				Sun and Zhu (2008)
	Qingdao	284–363	51–73	65–69	June–July	1900–2100 or 10–20 min after sunset	~50 or 80	Tchang and Koo (1936), Wu et al. (1994, 1995), and Watanabe et al. (1999)
	Xiamen	270–327	48–64	62–64	Apr–May, Aug			Zhang et al. (2006)
	Hong Kong	251–371	48–69	60–64				Chen et al. (2007)
B. *belcheri*	Xiamen	308–354	80–103	63–66	July, ?Sept			Zhang et al. (2006)
	Hong Kong	249–392	78–105	62–67				Chen et al. (2007)
	North Borneo (type locality)		69 and 80	66				Two specimens probably of name-bearing types, Nishikawa and Nishida (1997)
	Miri, North Borneo		75?–86	62–66				Nishikawa (unpublished data)

Xiamen and Hong Kong specimens with 62–64. This finding may be reminiscent of the so-called Jordan's rule that "in certain groups of fishes the northern or cold-water representatives have a larger number of vertebrae than those members which are found in tropical regions" (Jordan 1892, p. 107; also see McDowall 2008). This rule is often explained by a combination of genetic and environmental (thermal) factors, as shown in the number of abdominal vertebrae in *Oryzias latipes* by Yamahira and Nishida (2009). As the number of myomeres in *B. japonicum* is fixed by the end of the pelagic stage (Urata et al. 2007), its geographic variation in the myomere number may possibly be caused, even partly, by different water temperatures during the stages. Then, it follows that pelagic larvae derived from a local population may have a limited dispersal range with a thermal condition throughout a planktonic life of approximately 50 days or longer (see Table 27.1). Thus, a certain geographic differentiation is occurring among local populations, as inferred from genetic analyses using AFLP or microsatellite markers, although the mitochondrial sequence data almost deny such differentiations (Chen et al. 2007; Li et al. 2013). The somite (myomere) formation seems to be controlled by a common genetic mechanism, including the "segmentation clock" (Horikawa et al. 2006), mainly using Delta-Notch signaling, in lancelets and vertebrates (Beaster-Jones et al. 2008). Using a zebrafish mutant, the slowed segmentation clock was proved to reduce segment number by Schröter and Oates (2010). Therefore, the geographic variation in myomere number in *B. japonicum* may possibly be attributable in part to a 'clock disorder' influenced by water temperature.

27.3 *Asymmetron lucayanum* Complex Species A and B

The circumtropical shallow-water lancelets with gonads only on the right side and an urostyloid process (see Fig. 27.1b) have long been simply referred to as *A. lucayanum* (or *Epigonichthys lucayanus*, if the mentioned two genera are regarded as synonymous) with several junior synonyms (see Poss and Boschung 1996). In the Japanese waters, this nominal species [called 'onaga (long-tailed) namekuji-uo' in Japanese; Fig. 27.1b, c) has been recorded from Okinawa Island by Nishikawa (1979, 1980) and Urata and Ohtsuka (2014), the Kerama Islands (Nishikawa, unpublished data), Kuroshima Island in the Yaeyama Islands (Noda and Nishikawa 1989; Kuroyanagi and Nomura 2000), and Chichijima Island in the Ogasawara Islands (Tachikawa and Nishikawa 1997).

Kon et al. (2006) made a comprehensive molecular phylogenetic analysis using partial sequences of the mitochondrial COI gene from specimens collected globally and identified on obvious morphological basis as *Asymmetron lucayanum*, and found that they were markedly divided into three clades. Clades A and B were composed of Indo-West Pacific and West-Central Pacific samples, respectively, whereas clade C was represented by samples from Bermuda and Barbados in the West Atlantic (Fig. 27.2); high gene flow was implied within each clade, even between localities at distances of 2,000 to 10,000 km. Clade C is safely referable to

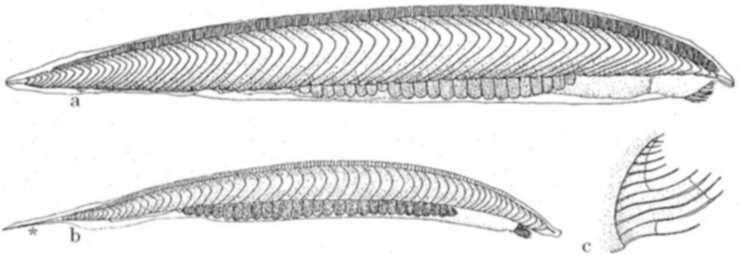

Fig. 27.1 Right side of whole body of *Epigonychtys maldivensis* (**a**) and *Asymmetron lucayanym* complex from Japanese waters (**b**), and enlarged view of buccal tentacles of the latter (**c**) to show an abrupt height change in intertentacular membrane. *Asterisk* shows urostyloid process (Modified from fig. 25.13 of Nishikawa 1995b)

A. lucayanum sensu stricto, because its type locality is Bimini and Nassau Harbor in the Bahamas (Andrews 1893), near Barbados, although nomenclatural considerations are now in progress on two other cryptic species. Kon et al. (2006) estimated the divergence time between sp. A and [sp. B + *A. lucayanum*] to be about 100 MYA, and that between sp. B and *A. lucayanum* about 12 MYA. The morphological stasis is really astonishing.

As the species A and B were found together on the shore of Kuroshima Island (Kon et al. 2006), comparative studies between them have been planned in embryology and ecology for a better understanding of their speciation and isolation, but so far in vain, because I have failed to collect any *Asymmetron* specimens there for these 10 years or so. The *Asymmetron lucayanum* species complex from other Japanese localities has not yet been surveyed using sufficient molecular information to be correctly identified at the specific level.

27.4 *Asymmetron inferum* (Japanese Name: geikotsu-namekuji-uo)

Nishikawa (2004) described a new lancelet, *A. inferum*, for the specimen collected from an anaerobic and sulfide-rich environment caused by decomposing sperm whale bodies at a depth of 229 m off Cape Nomamisaki, southwest end of Kyushu Island, Japan, as the first deep-water lancelet species. In morphology, this new species was unexpectedly similar to the shallow-water coral-sand-dwelling *A. lucayanum* complex (see Sect. 27.3) in every detail including the backward shift of the tentacular ring and the peculiar morphology of the intertentacular membrane (Fig. 27.1c) (see Nishikawa and Nishida 1997; Nishikawa 2004), only excepting the number of myomeres (83 in the former, instead of 55–72 in the latter). By the whole mitochondrial genome analyses (Kon et al. 2007), however, the distinction was proved quite remarkable with a unique gene rearrangement among the lancelets in *A. inferum*, although it was safely included in a well-

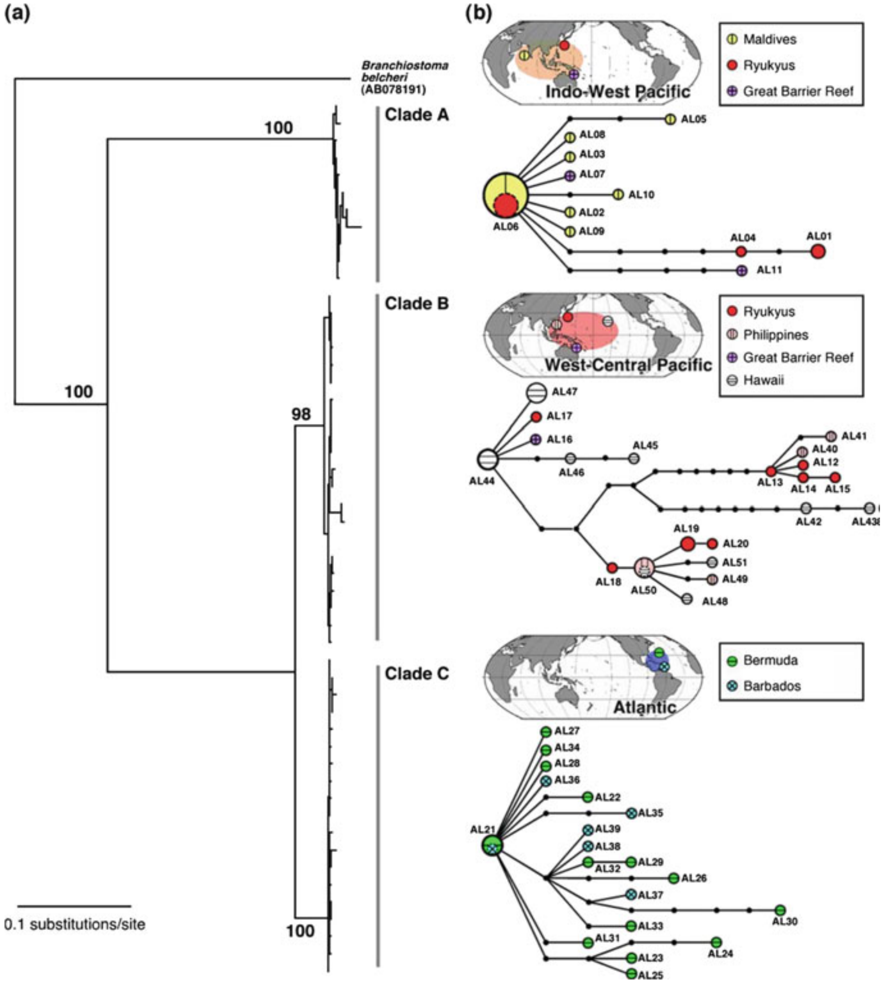

Fig. 27.2 (**a**) Cryptic speciation in the shallow-water *Asymmetron lucayanum* complex, as shown by a neighbor-joining tree of 39 haplotypes (62 specimens) from tropical waters over the world based on the COI gene (1035 bp); numbers beside major internal branches indicate bootstrap probabilities based on 1000 replicates. The outgroup "*Branchiostoma belcheri* (AB078191)" should be read as "*Branchiostoma japonicum* (AB078191)" (see Sect. 27.2). (**b**) Statistical parsimony network of its three clades (cryptic species), based on 1035 bp of the gene. Clade C is regarded as *A. lucayanm* sensu stricto. Each *circle* represents one haplotype: size of *circles* is proportional to haplotype frequency (1–20 specimens). *Circles* within *larger circles* (with *dotted outline*) represent haplotype sharing between two populations. *Solid-line circles* indicate the highest outgroup weight haplotype (Reproduced from the figure 3 of Kon et al. 2006 with permission of Springer)

defined clade together with *A. lucayanum* complex, distinct from *Branchiostoma* and *Epigonichthys* clades. *Asymmetron inferum* is sister to the shallow-water *A. lucayanum* complex (three species), constituting the most basal branch among this genus, with the estimated divergence time being 97–115 MYA.

Nishikawa (1981) reported a 10.3-mm-long pelagic larva with 84 myomeres obtained by towing in the surface layer (0–164 m) around the Senkaku Islands, southwest Japan. That number of myomeres is reminiscent of *A. inferum*, and therefore the larva may probably be assignable to it. Further finds of this species are thus expected from whale-fall (or other sulfide-rich) communities in the Far East.

27.5 *Epigonichthys maldivensis* (Japanese Name: kata-namekuji-uo)

Epigonichthys maldivensis (Fig. 27.1a) has been recorded in Japanese waters from Tanabe Bay and near Cape Shionomisaki, Kii Peninsula, and off Tanegashima Island, south of Kyushu Island (Nishikawa 1980), as well as Kuroshima Island in the Yaeyama Islands (Noda and Nishikawa 1989), with 67–69 myomeres. Its mitochondrial genome derived from the Kuroshima population has already been published (Nohara et al. 2005).

According to the global molecular phylogenetic analyses of this genus given by Kon et al. (in preparation; for abstract see Kon et al. 2011), many Indo-West Pacific populations, including that of Kuroshima, identified morphologically with *E. maldivensis*, constitute a single well-defined cluster with no marked differentiation. This species was established for a rarely collected four specimens from the Mahlosmadulu Atoll in the Maldive Islands by Cooper (1903). In the analyses of Kon et al., samples from the Maldives have not yet been included in spite of my several trials to obtain them, but the mentioned cluster is now composed of samples from Tanzania, West Indian Ocean, to New Caledonia, West Pacific. Therefore, the cluster may safely be assignable to *E. maldivensis*.

27.6 *Epigonichthys cultellus* (New Japanese Name: hime-kata-namekuji-uo)

Epigonichthys cultellus Peters, 1876 was established for the lancelets collected from Moreton Bay, East Australia (Peters 1876); my reexamination of the four name-bearing type specimens revealed the total myomere number to be 49–50, which are registered at the Museum für Naturkunde der Humboldt-Universität zu Berlin as ZMB1570 (three specimens) and ZMB1571 (one specimen). In the Far Eastern seas, this species has been recorded only from South China and Gulf of

Tonkin (=Beibu Gulf) by Tchang (1962) with 48–55 myomeres; its complete mitochondrial genome was recently determined for the South China population by Li et al. (2014).

Kon et al. (2004) collected an immature lancelet in 2003 with 54 myomeres (comparable with that number in *E. cultellus*) from Okinawa Island, but treated it as "genus and species *incertae sedis*" because of the lack of information as to gonadal arrangement and sequence data. According to the global molecular phylogenetic analyses of this genus by Kon et al. (see Sect. 27.5), many Indo-West Pacific samples including newly collected ones from Okinawa Island and Kuroshima Island, identified morphologically as *E. cultellus*, constitute a single cluster markedly distinct from other clusters. This cluster includes samples from the Great Barrier Reef and New Caledonia, although my collection efforts in the type locality (Moreton Bay) were unsuccessful, and therefore may safely be referable to *E. cultellus*. Thus, Kon et al.'s (2004) record from Okinawa Island can be allotted also to this species. This species has so far been collected only in the Ryukyus since 2003. A possible assumption may be that the species has a recent northward expansion of geographic distribution. Special attention should be paid to further occurrences of this species in all Japanese waters.

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References

Andrews EA (1893) An undescribed acraniate: *Asymmetron lucayanum*. Stud Biol Lab Johns Hopkins Univ 5:213–247

Andrews EA (1895) An amphioxus from Japan. Zool Anz 18:57–60

Beaster-Jones L, Kaltenbach SL, Koop D, Yuan S, Chastain R, Holland LZ (2008) Expression of somite segmentation genes in amphioxus: a clock without a wavefront? Dev Genes Evol 218:599–611

Chen Y, Cheung SG, Kong RYC, Shin PKS (2007) Morphological and molecular comparisons of dominant amphioxus populations in the China seas. Mar Biol 153:189–198

Chin TG (1941) Studies on the biology of the Amoy amphioxus *Branchiostoma belcheri* Gray. Philipp J Sci 75:369–424

Cooper CF (1903) Cephalochordata. I. Systematic and anatomical account. In: Gardiner JS (ed) The fauna and geography of the Maldive and Laccadive Archipelagos, vol 1. Cambridge University Press, Cambridge, pp 347–367

Gray JE (1847) Description of a new species of *Amphioxus* from Borneo. Proc Zool Soc Lond 15:35–36

Henmi Y, Yamaguchi T (2003a) Biology of the amphioxus *Branchiostoma belcheri* in the Ariake Sea, Japan. I. Population structure and growth. Zool Sci 20:897–906

Henmi Y, Yamaguchi T (2003b) Biology of the amphioxus *Branchiostoma belcheri* in the Ariake Sea, Japan II. Reproduction. Zool Sci 20:907–918

Horikawa K, Ishimatsu K, Yoshimoto E, Kondo S, Takeda H (2006) Noise-resistant and synchronized oscillation of the segmentation clock. Nature (Lond) 441:719–723

Japanese Association of Benthology (ed) (2012) Threatened animals of Japanese tidal flats: red data book of seashore benthos. Tokai University Press, Hadano

Jordan DS (1892) Relations of temperature to vertebrae among fishes. Proc Natl Mus 14:107–120

Kon T, Sakurai Y, Yoshino T (2004) A lancelet collected from Nakagusuku Bay, Okinawa Island. Biol Mag Okinawa 42:47–52

Kon T, Nohara M, Nishida M, Sterrer W, Nishikawa T (2006) Hidden ancient diversification in the circumtropical lancelet *Asymmetron lucayanum* complex. Mar Biol 149:875–883

Kon T, Nohara M, Yamanoue Y, Fujiwara Y, Nishida M, Nishikawa T (2007) Phylogenetic position of a whale-fall lancelet (Cephalochordata) inferred from whole mitochondrial genome sequences. BMC Evol Biol 7:127

Kon T, Nishida M, Nishikawa T (2011) A molecular phylogenetic analysis of the genus *Epigonichthys* (Cephalochordata) and the discovery of a species new to Japan. In: Abstracts of the 48th annual meeting of the Biological Society of Okinawa, University of the Ryukyus, Nishihara, 4 June 2011

Kuroyanagi K, Nomura K (2000) Population survey of a lancelet species, *Epigonichthys lucayanus* around Kuroshima Island, Yaeyama Group, the Southern Ryukyus. Nankiseibutu 42:85–88

Li WY, Zhong J, Wang YQ (2013) Genetic diversity and population structure of two lancelets along the coast of China. Zool Sci 30:83–91

Li WY, Fang SH, Wang YQ (2014) Complete mitochondrial genome of *Epigonichthys cultellus* (Cephalochordata: Branchiostomatidae). Zool Sci 31:766–772

McDowall RM (2008) Jordan's and other ecogeographical rules, and the vertebral number in fishes. J Biogeogr 35:501–508

Mizuta T, Kubokawa K (2004) Non-synchronous spawning behavior in laboratory-reared amphioxus *Branchiostoma belcheri* (Gray). J Exp Mar Biol Ecol 309:239–251

Nishikawa T (1979) A short report on the lancelet *Asymmetron lucayanum* Andrews, 1893 from Sesokojima Island, Okinawa. Biol Mag Okinawa 17:15–18

Nishikawa T (1980) Records of two lancelet species, *Asymmetron maldiense* and *A. lucayanum*, from the western Pacific. Publ Seto Mar Biol Lab 25:167–173

Nishikawa T (1981) Considerations on the taxonomic status of the lancelets of the genus *Branchiostoma* from the Japanese waters. Publ Seto Mar Biol Lab 26:135–156

Nishikawa T (1995a) Origin of the Japanese name "Namekuji-uo" (slug fish) for the lancelet, *Branchiostoma belcheri* Gray [Cephalochordata]. Nankiseibutu 37:41–46

Nishikawa T (1995b) Subphylum Cephalochordata. In: Nishimura S (ed) Guide to seashore animals of Japan with color pictures and keys, vol 2. Hoiku-sha, Osaka, pp 608–610

Nishikawa T (2004) A new deep-water lancelet (Cephalochordata) from off Cape Nomamisaki, SW Japan, with a proposal of the revised system recovering the genus *Asymmetron*. Zool Sci 21:1131–1136

Nishikawa T, Nishida M (1997) Problems in lancelet systematics. In: Kawashima S, Kikuyama S (eds) Advances in comparative endocrinology. 13th international conference of comparative endocrinology, Yokohama, 17–21 Nov 1997, vol 1. Monduzzi Editore, Bologna, pp 241–246

Noda H, Nishikawa T (1989) New finds of the two lancelet species, *Asymmetron lucayanum* and *A. maldivensis*, on the coast of Kuroshima Island, Yaeyama Islands. Nankiseibutu 31:37–38

Nohara M, Nishida M, Miya M, Nishikawa T (2005) Evolution of the mitochondrial genome in cephalochordates as inferred from complete nucleotide sequences from two *Epigonichthys* species. J Mol Evol 60:526–537

Pallas PS (1774) Spicilegia zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur, vol 1. G.A. Lange, Berlin

Peters W (1876) Über *Epigonichythys cultellus*, eine neue Gattung und Art der Leptocardii. Monatsber Berl Akad Wiss 1876:322–327

Poss SG, Boschung HT (1996) Lancelets (Cephalochordata: Branchiostomatidae): how many species are valid? Israel J Zool 42:S13–S66

Saotome K, Ojima Y (2001) Chromosomes of the lancelet *Branchiostoma belcheri* Gray. Zool Sci 18:683–686

Satoh N, Rokhsar D, Nishikawa T (2014) Chordata evolution and the three-phylum system. Proc R Soc B 281:1729 doi :10.1098/rspb.2014.1729

Schröter C, Oates AC (2010) Segment number and axial identity in a segmentation clock period mutant. Curr Biol 20:1254–1258

Sun YM, Zhu Q (2008) The morphology and taxonomy of amphioxus in the coastal waters of Weihai. Mar Sci 32(9):18–24

Tachikawa H, Nishikawa T (1997) First finds of the circum-tropical lancelet *Epigonichthys lucayanus* (Andrews) from Chichijima Island, Ogasawara Islands, Japan (Cephalochordata). Nankiseibutu 39:145

Tchang S (1962) Sur la presence du genre *Asymmetron* dans la mer de Chine et la distribution géographique de *Branchiostoma belcheri* (Gray). Acta Zool Sin 14:525–528

Tchang S, Koo KC (1936) Description of a new variety of *Branchiostoma belcheri* Gray from Kiaochow Bay, Shantung, China. Contrib Inst Zool Nata Acad Peiping 3(4):77–114

Ueda H, Kamakura H (2006) Synchronous recruitment and growth pattern of planktonic larvae of the amphioxus *Branchiostoma belcheri* in the Seto Inland Sea, Japan. Mar Biol 148:1263–1271

Urata M, Ohtsuka S (2014) Occurrence of *Asymmetron lucayanum* Andrews, 1893 complex off Naha, Okinawa. Bull Setouchi Field Sci Center Grad Sch Biosph Sci Hiroshima Univ 12:21–25

Urata M, Yamaguchi N, Henmi Y, Yasui K (2007) Larval development of the oriental lancelet, *Branchiostoma belcheri*, in laboratory mass culture. Zool Sci 24:787–797

Wang YQ, Fang SH (2005) Taxonomic and molecular phylogenetic studies of amphioxus: a review and prospective evaluation. Zool Res 26:666–672

Wang YQ, Xu QS, Peng XX, Zhou HT (2004) Taxonomic status of amphioxus *Branchiostoma belcheri* in Xiamen beach estimated by homologous sequences of Cyt *b* gene. Acta Zool Sin 50:202–208

Watanabe T, Yoshida M, Shirai H (1999) Effect of light on the time of spawning in the amphioxus, *Branchiostoma belcheri tsingtauense*. Contrib Ushimado Mar Lab Okayama Univ 37:1–7

Wu XH, Zhang SC, Wang YY, Zhang BL, Qu YM, Jiang XJ (1994) Laboratory observation of spawning, fecundity and larval development of amphioxus (*Branchiostoma belcheri tsingtauense*). Chin J Oceanol Limnol 12:289–294

Wu XH, Zhang SC, Wang YY, Zhang BL, Qu YM, Jiang XJ (1995) The life history of *Branchiostoma belcheri tsingtauense*: age, growth and death. Oceanol Limnol Sin 26:175–178

Xiao YS, Zhang Y, Gao TX, Yabe M, Sakurai Y (2008) Phylogenetic relationships of the lancelets of the genus *Branchiostoma* in China inferred from mitochondrial genome analysis. Afr J Biotechnol 7:3845–3852

Xu QS, Ma F, Wang YQ (2005) Morphological and 12S rRNA gene comparison of two *Branchiostoma* species in Xiamen waters. J Exp Zool (Mol Dev) 304B:1–9

Yamahira K, Nishida T (2009) Latitudinal variation in axial patterning of the medaka (Actinopterygii: Adrianichthyidae); Jordan's rule is substantiated by genetic variation in abdominal vertebral number. Biol J Linn Soc 96:856–866

Yan LN, Zho HK, Cao YP (2005) Divergence in Qinhuangdao, Qingdao and Xiamen geographical populations of amphioxus (*Branchiostoma belcheri* Gray) based on morphological character analysis. Zool Res 26:311–316

Yasui K, Kubokawa K (2005) Biology of cephalochordate lancelet. University of Tokyo Press, Tokyo

Zhang QJ, Zhong J, Fang SH, Wang YQ (2006) *Branchiostoma japonicum* and *B. belcheri* are distinct lancelets (Cephalochordata) in Xiamen waters in China. Zool Sci 23:573–579

Zhang QJ, Li G, Sun Y, Wang YQ (2009) Chromosome preparation and preliminary observation of two amphioxus species in Xiamen. Zool Res 30:131–136

Zhao Q, Zhu Q (2011) Taxonomic and genetic status of lancelet in Weihai coastal waters based on mitochondrial DNA sequence. Chin J Oceanol Limnol 29:623–632

Zhong J, Zhang QJ, Xu QS, Schubert M, Laudet V, Wang YQ (2009) Complete mitochondrial genomes defining two distinct lancelet species in the West Pacific Ocean. Mar Biol Res 5:278–285

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